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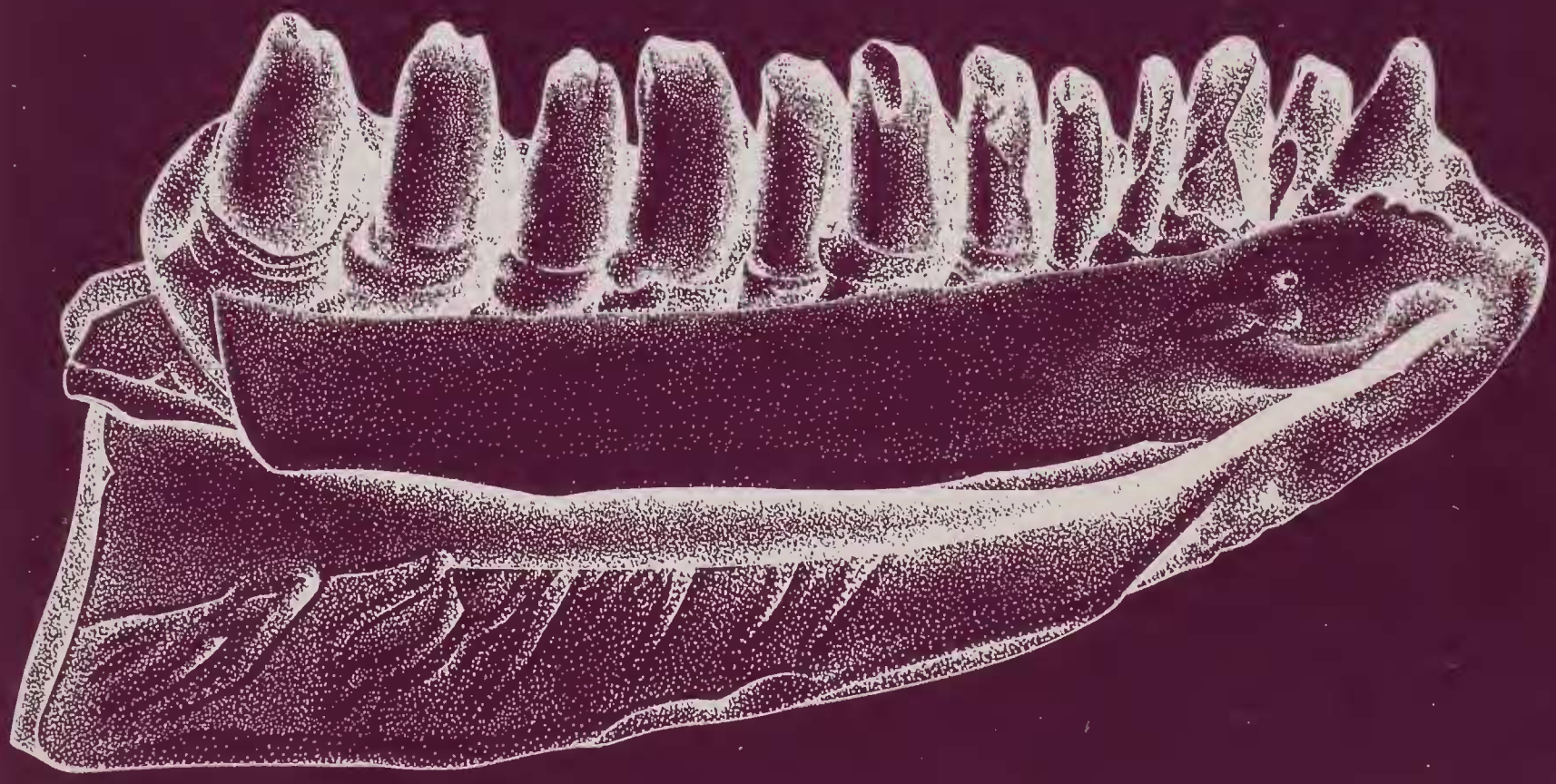

TAXONOMY AND EVOLUTION OF LATE CRETACEOUS LIZARDS (REPTILIA: SQUAMATA) FROM WESTERN CANADA

GAO KEQIN and RICHARD C. FOX

NUMBER 33

PITTSBURGH, 1996

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TAXONOMY AND EVOLUTION OF LATE CRETACEOUS LIZARDS (REPTILIA: SQUAMATA) FROM WESTERN CANADA

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Cover illustration: *Glyptogenys ornata,* Oldman Formation, Alberta: UALVP 29735 (holotype), incomplete left dentary, medial view (see Fig. 12, lower illustration).

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Contents

Abstract 1
Introduction 2
Materials and Methods 3
Geological Setting 6
Dental Morphology and Terminology 10
Systematic Paleontology 13
Order Squamata Oppel, 1811 13
Suborder Lacertila Owen, 1842 13
Infraorder Iguania Cuvier, 1807 13
Family Iguanidae* Gray, 1827 13
Genus *Cnephasaurus,* **new genus** 13
Genus and species new (A) 16
Genus and species new (B) 17
Infraorder Scincomorpha Camp, 1923 18
Family Teiidae Gray, 1827 18
Genus *Chamops* Marsh, 1892 19
Genus *Socognathus* Gao and Fox, 1991 25
Genus *Sphenosiagon* Gao and Fox, 1991 28
Genus *Glyptogenys* Gao and Fox, 1991 31
Genus *Gerontoseps* Gao and Fox, 1991 33
Genus *Leptochamops* Estes, 1964 36
Genus *Meniscognathus* Estes, 1964 40
Genus *Haptosphenus* Estes, 1964 42
Genus *Stypodontosaurus,* **new genus** 45
Family Scincidae Gray, 1825 46
Genus *Penemabuya,* **new genus** 46
Genus *Orthrioscincus,* **new genus** 49
Genus *Aocnodromeus,* **new genus** 51
Family ?Xantusiidae Baird, 1859 53
Genus and species new (unnamed) 54
Genus *Contogenys* Estes, 1969 55
Family ?Cordylidae Gray, 1837 58
Genus and species undetermined (A) 58
Genus and species undetermined (B) 60
Family incertae sedis 60
Genus and species new (A) 60
Genus and species new (B) 61
Genus and species undetermined 62
Infraorder Anguimorpha Fürbringer, 1900 62
Family Xenosauridae Cope, 1886 62
Genus and species undetermined 66
Family Anguidae Gray, 1825 67
Genus *Odaxosaurus* Gilmore, 1928 67
Genus and species undetermined 73
Family Necrosauridae* Hoffstetter, 1943 74
Genus *Colpodontosaurus* Estes, 1964 74
Genus and species new (unnamed) 75
Genus *Parasaniwa* Gilmore, 1928 76
Family Helodermatidae Gray, 1837 81
Genus *Paraderma* Estes, 1964 82
Genus *Labrodioctes,* **new genus** 86

Genus and species undetermined 88
Family Varanidae Gray, 1827 89
Genus *Palaeosaniwa* Gilmore, 1928 90
Geological Distribution and Evolution of Late Cretaceous Lizards in Western Canada 94
Conclusions 99
Acknowledgments 100
Literature Cited 100

ABSTRACT

Upper Cretaceous nonmarine deposits of western Canada have yielded fossil lizards representing some 40 species in some 30 genera and ten families. Hundreds of specimens from geological formations of Aquilan, Judithian, and Lancian age (Campanian–Maastrichtian) reveal previously unknown aspects of the evolutionary history of several lizard families during the last 18 Myr of the Cretaceous Period in western Canada. Among these lizards, iguanids are described for the first time from the Upper Cretaceous in North America, and primitive scincids, anguids, and possible cordylids are recorded there, as well.

On the basis of taxonomic composition and geological age, three assemblages are recognizable: 1) An Aquilan (early Campanian) assemblage, known from the Milk River Formation, documents an early diversification of the Iguanidae*, Scincidae, Xenosauridae, Anguidae, and Necrosauridae*, whereas the Teiidae are poorly recorded. 2) A Judithian (mid-Campanian) assemblage, from the Oldman Formation, is composed predominantly of teiids; these are substantially different taxonomically from teiids of Lancian age and, hence, represent a distinct evolutionary stage of the family (this result is contrary to that of previous authors, but is comparable to mammalian patterns of evolution over the same interval). This assemblage also includes the earliest records of the Helodermatidae and Varanidae in North America. 3) A Lancian (late Maastrichtian) assemblage, from the Frenchman and Scollard formations, is virtually identical to that of the type Lance Formation, Wyoming, but includes specimens of several new taxa, and others that allow taxonomic revisions of several species previously known from outside the study area. These newly discovered lizards represent important components of the North American Late Cretaceous nonmammalian vertebrate fauna, and a taxonomic treatment of these lizards gives a more nearly complete picture and a better understanding of the evolutionary history of the relevant lizard families than was possible before.

INTRODUCTION

Lizards are the most successful modern reptiles in terms of their great taxonomic and ecologic diversities, and wide geographical distribution. Osteologically, the group can only be diagnosed as primitive squamates lacking the specializations of amphisbaenians and snakes, but retaining such plesiomorphic character states as loss of the lower temporal bar and development of a highly mobile joint between the quadrate and squamosal, a condition commonly termed streptostyly. The true lizards in the sense of Estes (1983*a*, 1983*b*) can be traced back to the Late Jurassic, but no lizards of this age can be referred to any modern lizard family, although infraordinal relationships with Recent groups can be determined. Early Cretaceous lizard fossils are poorly known, partly because of the worldwide transgression that submerged about one-third of the present land area of the Earth (Dott and Batten, 1988; also see Funnell, 1990). However, several recent discoveries have added significantly to the lizard fossil record of this age; these new discoveries include fossil materials from Central Asia (Nessov, 1985, 1988), Mongolia (Alifanov, 1989; M. A. Norell, personal communication, 1993), Texas (Murry et al., 1989; Winkler et al., 1990), and from southern Utah (R. L. Cifelli, personal communication, 1991). Study of Late Cretaceous lizard fossils is especially significant, since the Late Cretaceous appears to have been an important period for the establishment and early diversification of most modern lizard families (Estes, 1983*b*); furthermore, the widely exposed fossiliferous nonmarine deposits of this age in the Western Interior of North America and use of highly productive screen-washing techniques for recovery of small vertebrate fossils (Hatcher, 1896; McKenna, 1960; Clemens, 1963; Lillegraven, 1969) have provided a unique advantage in undertaking this study.

In North America, the first discovery of fossil lizards from the Upper Cretaceous was associated with paleontological exploration during the period 1889–1892 in Converse County (now Niobrara County), Wyoming. Marsh (1892) made the first report of Late Cretaceous terrestrial lizard fossils, naming *Chamops segnis* (based on an incomplete dentary) and *Iguanavus teres* (based on several vertebrae) from the "Laramie Formation" of Wyoming (the "Laramie Formation" was later renamed [Stanton, 1910] as the Lance Formation). Work since has shown that *Chamops segnis* is a common Late Cretaceous teiid and *Iguanavus teres* is possibly the synonym of the former (Estes, 1964, 1983*a*), or a nomen dubium as treated in this paper. During this early period, although several thousand isolated teeth, jaws, and other materials of a variety of vertebrates had been found by J. B. Hatcher (chief collector for O. C. Marsh) and his assistants (based on these materials, for example, Marsh named 18 new genera and 32 species of mammals), no special attention was paid to lizards except for the two forms mentioned above (Gilmore, 1928).

Gilmore (1928) made the pioneer contribution to the systematic study of Late Cretaceous lizards from North America. In his monograph "Fossil Lizards of North America," Gilmore described 17 species in 12 genera from the Lance Formation of Wyoming and equivalent beds elsewhere; among these, 13 species in ten genera were new, and the names of seven genera and species are still valid today, with the others having been emended since (Estes, 1964, 1983*a*). Few subsequent papers in this field were published, until Estes' (1964) comprehensive work on small nonmammalian vertebrates from the Lance Formation, Wyoming. Other North American Late Cretaceous lizards were described by Estes et al. (1969) from the Hell Creek Formation, Montana; Sahni (1972) from the Judith River Formation, Montana; and Armstrong-Ziegler (1978, 1980) and Sullivan (1981) from the Fruitland Formation, New Mexico. Recent discoveries also include undescribed materials from New Jersey (Parris and Grandstaff, 1989; Denton et al., 1991), Utah (R. L. Cifelli, personal communication, 1991; Eaton, 1993), and from Texas (Rowe et al., 1992). Estes (1983*a*) provided the first and the most recent taxonomic codification of the data on all fossil lizards known at the time: his "Sauria terrestria, Amphisbaenia" contribution to the "Handbuch der Paläoherpetologie" included 18 species in 17 genera of Late Cretaceous lizards from North America.

In western Canada, early discoveries of Late Cretaceous terrestrial lizards were coincident with a period of the "Great Canadian Dinosaur Rush," from 1912 to 1925 (see Koster et al., 1987). Gilmore (1923) marked the first report of Late Cretaceous lizards from western Canada by referring a nearly complete dorsal vertebra (UA 112) to a "lacertian" (= lacertilian). The specimen was found by G. F. Sternberg in 1921, at Sandy Point, South Saskatchewan River, near Empress, southeastern Alberta (Belly River Formation, now Oldman Formation; Russell and Landes, 1940). Later reports of Creta-

ceous lizards from western Canada were given in descriptive papers by C. M. Sternberg (1951), Waldman (1970), and Gao and Fox (1991); and in faunal lists by L. S. Russell (1935, 1964), Russell and Landes (1940), Fox (1972*a*, 1976, 1989), Currie (1986), Eberth (1987), and Koster et al. (1987).

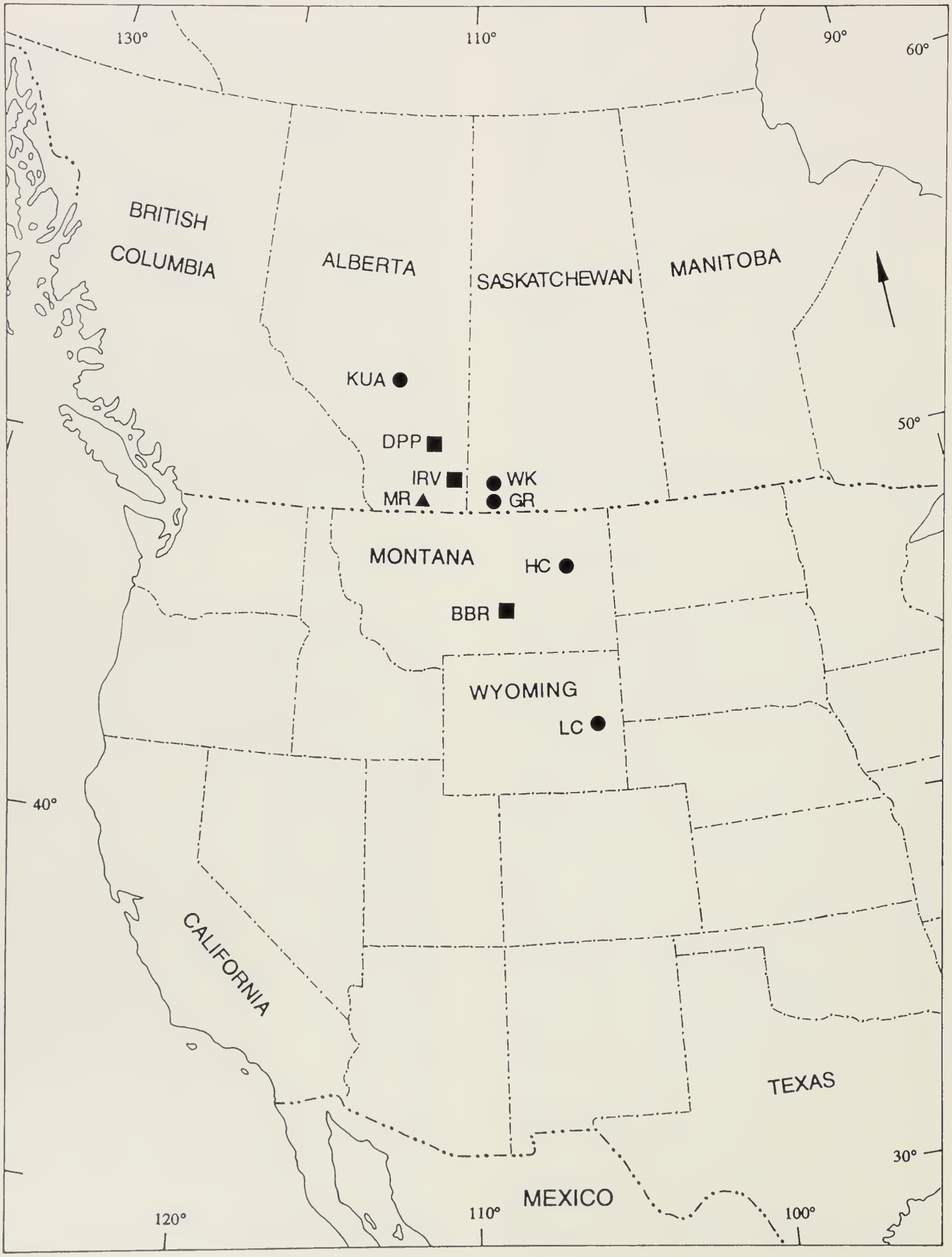
This study focuses on fossil lizards from localities in geologic formations of Aquilan, Judithian, and Lancian age (NALMA = North American Land Mammal Age, see L. S. Russell, 1964; Lillegraven and McKenna, 1986) in western Canada (see Fig. 1), covering a geologic span of approximately 18 Myr (Lillegraven and McKenna, 1986; Harland et al., 1990). However, the major concern of this study is the fossil lizards from the Oldman and Milk River formations. The former formation is about 11 Myr and the latter 18 Myr earlier than the Lance and Hell Creek formations (Lillegraven and McKenna, 1986; Harland et al., 1990). The fossil lizards from the Oldman Formation (Judithian) indicate that the Judithian lizard assemblage is substantially different from that of Lancian age, contrary to the conclusions of previous authors (see Sahni, 1972; Armstrong-Ziegler, 1978, 1980; Sullivan, 1981; Estes, 1983*a*). This study shows that most lizard specimens from the Oldman Formation are representives of new genera and new species. Some are referrable to genera occurring in Lancian horizons, but none can be definitely assigned to Lancian species. This result is consistent with the mammalian evidence that shows less than five percent of mammalian species of Judithian age are the same as those from Lancian horizons (see Lillegraven and McKenna, 1986). The Milk River (Aquilan) lizards document an early diversification of several modern families, especially Scincidae, and include the earliest known North American record of the Iguanidae*. These newly discovered lizards represent important components of the North American Late Cretaceous nonmammalian vertebrate fauna, and a study of these lizards gives a more nearly complete picture and a better understanding of the taxonomic and evolutionary history of the relevant lizard families than was previously possible.

MATERIALS AND METHODS

This study is based mainly on fossils collected from the Upper Cretaceous Milk River, Oldman, Frenchman, and Scollard formations, western Canada; but some specimens from the Lance and Hell Creek formations in the United States are also included because they provide new information for a better understanding of the relevant taxa, and provide materials for recognition of new taxa that have close relatives in the study area. The specimens from the Milk River Formation were collected by UALVP field parties from 1968 to 1970. The Oldman specimens are in the collections of both UALVP and RTMP, from several localites in southern Alberta, made from 1966 to the present. The specimens from the Frenchman Formation were collected by the SMNH and UALVP parties from 1979 to 1984. All the new materials from the Lance and Hell Creek formations used in this study are in the UALVP collections, obtained from field work in 1969–1976. Finally, the UALVP Scollard lizards were recently sorted from screened concentrate originally collected during 1964–1967 by University of Kansas field parties (Lillegraven, 1969).

The specimens used in this study are mostly tooth-bearing maxillaries and dentaries. These provide materials for the recognition of a number of new taxa of lizards, as well as assistance in understanding the phylogenetic relationships of several previously known species. Other materials in the available collections include disarticulated skull elements, such as frontals, parietals, jugals, pterygoids, premaxillaries (see Fig. 2 for anatomical positions), and disarticulated vertebrae and limb bones. These latter elements in most cases are unreliable for identification at generic and specific levels without reference to articulated skulls or skeletons, with the exception of certain groups (e.g., Xenosauridae) in which the disarticulated skull elements show a species-specific sculpture pattern. The identification of jaw material is based mainly on dental morphology (tooth form and cusp pattern) and general jaw configuration. Tooth form and cusp pattern are also important for ecological interpretations, as several studies (Lonnberg, 1903; Schmidt, 1919; Cowles, 1930; Hotton, 1955; Presch, 1974*b*; Greene, 1982; Estes and Williams, 1984) have shown the connections between dental morphology and food preference of lizards, and these studies have demonstrated that the tooth type and the particular cusp pattern as well as the pattern of wear provide indirect evidence as to the possible habit and diet of the lizards.

Most of the specimens for this study have been obtained through screen washing in the field and in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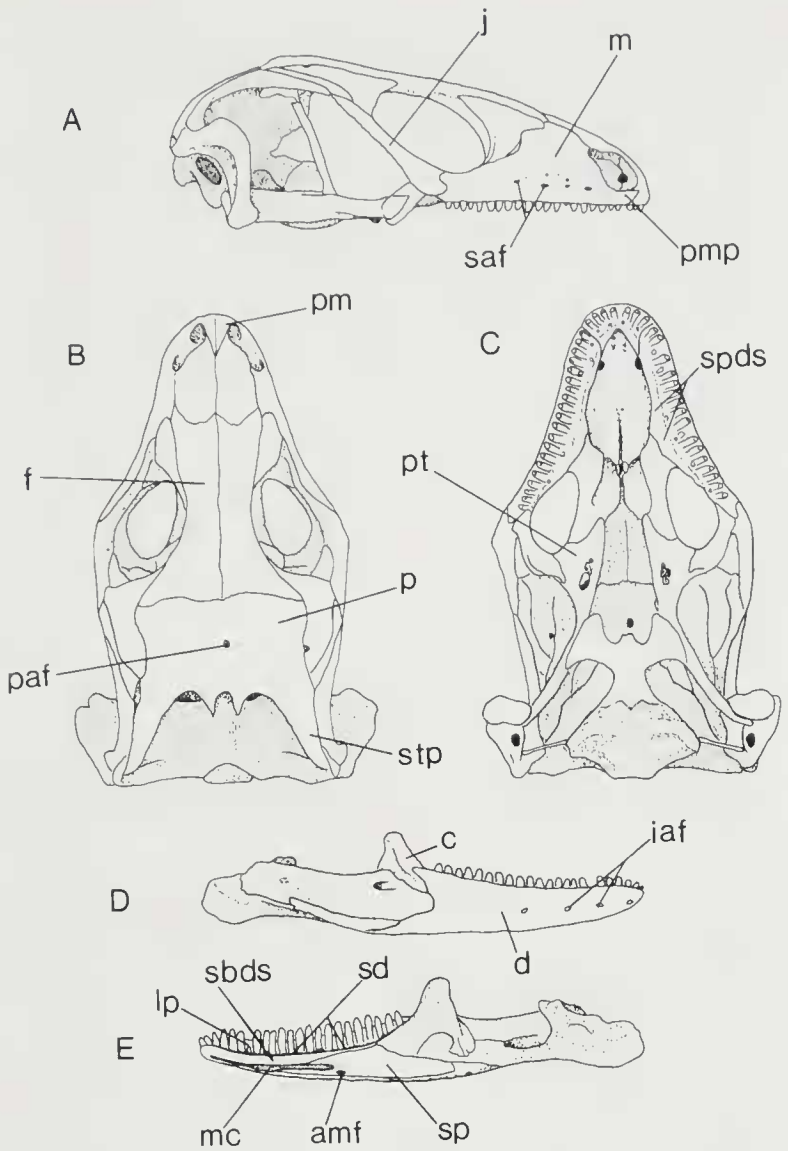

Fig. 2.—Skull and mandible of *Eumeces obsoletus* (Scincidae), showing anatomical structures of lizards (after Estes et al., 1988). A–C, skull in lateral, dorsal, and ventral views; D, E, mandible in lateral and medial views. Abbreviations for this and all subsequent figures: aif, anterior inferior alveolar foramen; amf, anterior mylohyoid foramen; c, coronoid; d, dentary; f, frontal; iaf, inferior alveolar foramen; ims, intramandibular septum; j, jugal; lp, lateral parapet of dentary; m, maxillary; mc, Meckelian canal; p, parietal; paf, parietal foramen; pm, premaxillary; pmp, premaxillary process; pt, pterygoid; saf, superior alveolar foramen; sbds, subdental shelf; sd, sulcus dentalis; sp, splenial; spds, supradental shelf; stp, supratemporal process of parietal.

the laboratory, with some relatively large specimens collected by surface picking from outcrops. When necessary, specimens were prepared manually under a Wild M-7 microscope in the laboratory. All holotypes and well-preserved specimens are illustrated in photoplates or outline drawings. The specimens were coated with magnesium chloride, and the photographs were taken using an Olympus OM-2s camera with 50 mm macro lens and bellows. The textfigures were drawn with assistance of a camera lucida. All measurements of the specimens are in millimeters.

Institutional abbreviations: AMNH—American Museum of Natural History, New York, New York; ANSP—Academy of Natural Sciences, Philadelphia, Pennsylvania; CMN (= NMC)—Canadian Museum of Nature (= National Museum of Canada), Ottawa, Ontario; GSC—Geological Survey of Canada, Ottawa, Ontario; MCZ—Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts; MNA—Museum of Northern Arizona, Flagstaff, Arizona; RTMP—Royal Tyrrell Museum of Palaeontology, Drumheller, Alberta; SMNH—Saskatchewan Museum of Natural History, Regina, Saskatchewan; SMU—Southern Methodist University, Dallas, Texas; UALP—Laboratory of Paleontology, University of Arizona, Tucson, Arizona; UALVP (= UA)—Laboratory for Vertebrate Paleontology, Department of Biological Sciences, University of Alberta, Edmonton, Alberta; UCMP (= UC)—Museum of Paleontology, University of California, Berkeley, California; UMMZ—Museum of Zoology, University of Michigan, Ann Arbor, Michigan; UNM—University of New Mexico, Albuquerque, New Mexico; USNM (= NMNH)—United States National Museum (= National Museum of Natural History, Smithsonian Institution), Washington, D.C.; YPM (= YUM)—Yale Peabody Museum, New Haven, Connecticut; YPM-PU—"Princeton Collection" now housed in Yale Peabody Museum; ZPAL—Institute of Paleobiology, Polish Academy of Sciences, Warsaw, Poland.

Locality abbreviations: AB—Altman Blowout (= UCMP loc. V-5616; Clemens, 1963), Lance Formation, Lance Creek, Niobrara County, Wyoming; BB—Bonebed microfossil sites in Dinosaur Provincial Park (see Brinkman, 1990; Eberth, 1990*b*); BBR—Blackbird Ridge site (NW 1/4, Sec. 6, Tp. 7, R 20), Judith River Formation, Golden Valley County, Montana; BCA—Bug Creek Anthills (Sloan and Van Valen, 1965; Estes et al., 1969), Hell Creek Formation, McCone County, eastern Montana; BTB—Bushy Tailed Blowout (= UCMP

←

Fig. 1.—Geographical distribution of the Upper Cretaceous lizard localities (selected) in western Canada and nearby areas (Montana and Wyoming). Solid triangle indicates Aquilan locality in the Milk River Formation, Alberta; solid squares indicate Judithian localities of the Oldman and Judith River formations, Alberta and Montana; solid dots indicate Lancian localities of the Scollard (Alberta), Frenchman (Saskatchewan), Hell Creek (Montana), and Lance (Wyoming) formations. Abbreviations as listed in Materials and Methods.

loc. V-5711; Clemens, 1963), Lance Formation, Lance Creek, Niobrara County, Wyoming; DPP—Dinosaur Provincial Park (see, e.g., Dodson, 1987; Eberth, 1990*b*), Oldman Formation, Alberta; GR—Gryde locality (Tokaryk and James, 1989; Storer, 1991), Frenchman Formation, Frenchman River Valley, southwestern Saskatchewan; HC—Hell Creek Formation, McCone County, Montana (see BCA above); IRV—Irvine locality (Fox, 1968), Oldman Formation, southeastern Alberta; KUA—The University of Kansas, Alberta localities (Clemens and Russell, 1965; Lillegraven, 1969), Scollard Formation, Red Deer River Valley near Scollard, central Alberta; LC—Lance Creek Valley and environs (see Clemens, 1963), various localities of the Lance Formation, Niobrara County, Wyoming; MR—UALVP Milk River localities (Fox, 1972*a*), Milk River Formation, southern Alberta; WK—Wounded Knee locality (Fox, 1989), Frenchman Formation, Frenchman River Valley, southwestern Saskatchewan.

GEOLOGICAL SETTING

The specimens used in this study were collected from three horizons, chronologically from oldest to youngest: the upper member of the Milk River Formation (Dowling, 1917; Russell and Landes, 1940), early Campanian (Williams and Burke, 1964; Fox, 1976; Lillegraven, 1991) or Aquilan (NALMA, L. S. Russell, 1964; Lillegraven and McKenna, 1986) in age; the Oldman Formation (Russell and Landes, 1940), mid-Campanian (L. S. Russell, 1975; Eberth, 1987) or Judithian (NALMA, L. S. Russell, 1964; Lillegraven and McKenna, 1986) in age; and the Frenchman Formation (Furnival, 1946) and its equivalent Scollard (Irish, 1970; Gibson, 1977; Lerbekmo and Coulter, 1985), Lance (Stanton, 1910) and Hell Creek (Brown, 1907) formations, all late Maastrichtian or Lancian (Dorf, 1942; L. S. Russell, 1964; Lillegraven and McKenna, 1986) in age. These formations accumulated on the coastal plain adjacent to the Western Interior Seaway during Campanian–Maastrichtian time. The main source of these sediments was from the then-uplifting Rocky Mountains (Price and Mountjoy, 1970; Rahmani and Lerbekmo, 1975; Eberth, 1990*a*) west of the seaway.

Paleogeography and Depositional History

At the time when the upper member of the Milk River Formation was deposited (early Campanian), the North American continent was divided by the Western Interior Seaway, which extended from north to south along the eastern side of the Rocky Mountains and linked the Arctic Ocean with the Gulf of Mexico (see, e.g., Williams and Stelck, 1975; Funnell, 1990; Nicholls and Russell, 1990). The shallow epeiric sea covered most of what is now Alberta, southeastern Saskatchewan, eastern Montana, Wyoming, Colorado, northeastern New Mexico, and Texas. In western Canada, continental deposits of that age are exposed only in southern Alberta.

By mid-Campanian time, the rising Rocky Mountains caused the retreat of the Interior Sea to the east and the deposition of detritus in the Mackenzie River valley of the Northwest Territories, in Alberta and Saskatchewan, and in Montana, Wyoming, and New Mexico (Williams and Stelck, 1975:text-fig. 7; Funnell, 1990:fig. 11). The Oldman Formation and the upper part of the Judith River Formation, Montana, were formed at about the same time. Lizard fossil-bearing deposits of the same age are also known from New Jersey, one of the few occurrences of nonmarine vertebrates on the eastern side of the Late Cretaceous epeiric seaway (Parris and Grandstaff, 1989; Denton et al., 1991).

By late Campanian and early Maastrichtian time, the last major transgression of the Interior Sea (Bearpaw Sea; see Caldwell et al., 1978) covered a large area including Alberta north of the Peace River Arch (Wall, 1975) and west to the edge of the foothills in southern Alberta and Montana (Williams and Stelck, 1975). Continental deposits were developed in central and western Alberta, and in central Saskatchewan (Edmonton Group and St. Mary River Formation); however, lizard fossils are rarely recovered from these deposits, except for a *Chamops*-like teiid from the Wapiti Formation, northwestern Alberta (see later discussion). In northwestern New Mexico and southwestern Colorado, the Fruitland Formation was probably deposited at about this time: the age of the formation has been determined as Judithian, based on pollen (Fassett and Hinds, 1971), ammonites, and radiometric dating (Cobban, 1973; Fassett, 1987; Brookins and Rigby, 1987), and vertebrate faunal comparison with Lancian and Judithian assemblages from Wyoming and Montana (L. S. Russell, 1975; Fox, 1978; Armstrong-Ziegler,

1980; Lillegraven and McKenna, 1986; Lucas et al., 1987; Rigby and Wolberg, 1987); but more recently as Edmontonian on mammalian fossils (Lillegraven and Ostresh, 1990).

In the latest Cretaceous, overfilling of sediments from the west accompanying uplift in the Mackenzie Mountains region caused the regression of the late Maastrichtian Sea from the Western Interior (Williams and Stelck, 1975). At the same time, extensive clastic deposits were developed in Alberta (Scollard Formation), Saskatchewan (Frenchman Formation), Wyoming (Lance Formation), and Montana (Hell Creek Formation). A rich fossil vertebrate fauna, including a large number of lizard taxa, has been found in these deposits.

Geological Formations

Within the study area, Upper Cretaceous nonmarine deposits are composed mainly of sandstones, siltstones, and shales, and are extensively exposed along the river valleys and occasionally in badlands. Various authors have given detailed descriptions of these deposits; the lizard fossil-bearing sediments include the following formations (see Fig. 3 for correlations):

Milk River Formation.—Exposed along the Milk River and its tributaries in southern Alberta, the Milk River Formation is approximately equivalent to the Eagle Formation of Montana. Having a maximum thickness of about 77 m (Russell and Landes, 1940), the Milk River Formation can be subdivided into upper and lower members. The lower member (maximum thickness of 41 m) is dominantly marine in origin, characterized by dark shales grading upward into medium-grained sandstones with concretions. The upper member is composed of nonmarine, drab gray, brown, and dark gray argillaceous sandstones and sandy shale with streaks of impure lignite (Russell and Landes, 1940; Crockford and Clow, 1965). The upper member is about 36 m in maximum thickness (Russell and Landes, 1940) and is Aquilan (early Campanian) in age (L. S. Russell, 1964; Fox, 1976; Lillegraven, 1991). L. S. Russell (1935) recorded the discovery of fossil molluscs and vertebrates from the upper member of the Milk River Formation, from which a fragmentary dentary (GSC 8721) was listed as "Lacertilia incertae sedis." Recently, Fox (1968, 1969, 1970, 1971, 1972*a*, 1972*b*, 1984, 1985) reported a series of discoveries of mammalian fossils from the upper member of the formation exposed in Verdigris Coulee, including the geologically youngest triconodonts and symmetrodonts, primitive lipotyphlan insectivores, and diverse early marsupials. Fox (1972*a*) also published a faunal list, which included six lizard taxa associated with those of elasmobranchs, actinopterygian fishes, salamanders, turtles, champsosaurs, crocodiles, dinosaurs, and mammals. The lizards are described here for the first time.

Oldman Formation.—The Oldman Formation is composed of nonmarine deposits in Alberta that correlate with the upper part of the Judith River Formation of Montana (L. S. Russell, 1964; Eberth, 1987; Thomas et al., 1990). The name "Oldman Formation" was proposed by Russell and Landes (1940) as the substitute for the commonly called "Pale beds" and the upper division of Dawson's (1881) Belly River series. McLean (1971, 1977) recommended to drop the "Oldman" from the nomenclature and extend the use of "Judith River" into the Alberta area. This motion has been followed by some authors but rejected by others (e.g., Rahmani and Lerbekmo, 1975; Fox, 1976, 1978; see also Eberth and Hamblin, 1993). In the current relevant literature, both "Oldman" and "upper Judith River" are used for the same geologic formation in Alberta.

The name "Oldman Formation" remains in this paper as Russell and Landes (1940) defined it, for its convenient use as a geographically extensive, lithologically mappable unit (J. F. Lerbekmo, personal communication, 1989). The characteristic rocks of this formation are pale gray bentonitic sandstones, with interbedded gray and brown shales; coal seams are seen only at the top of the formation (L. S. Russell, 1964). The outcrops of the formation are widely exposed along the Milk River and the South Saskatchewan River north of Medicine Hat, and are best exposed in the Dinosaur Provincial Park along the Red Deer River north of Brooks. The thickness of the formation as known from drilling is about 127 m in the Irvine area, increasing southward to about 180 m in the Manyberries area (Crockford and Clow, 1965). The formation has yielded radiometric dates of about 76 Myr (Thomas et al., 1990) and a large vertebrate fauna (summarized in L. S. Russell, 1964; Langston, 1965; Fox, 1976; Currie, 1986; Eberth, 1987; and Koster et al., 1987). Within the uppermost 100 m of the formation, a recently recognized disconformity reflects a major Campanian uplift event in the Cordillera (Eberth, 1990*a*, 1990*b*), and the deposits above this disconformity have been recently named as the Dinosaur Park Formation (Eberth and Hamblin, 1993). Recent studies of the 24 microfossil localities above and below the disconformity

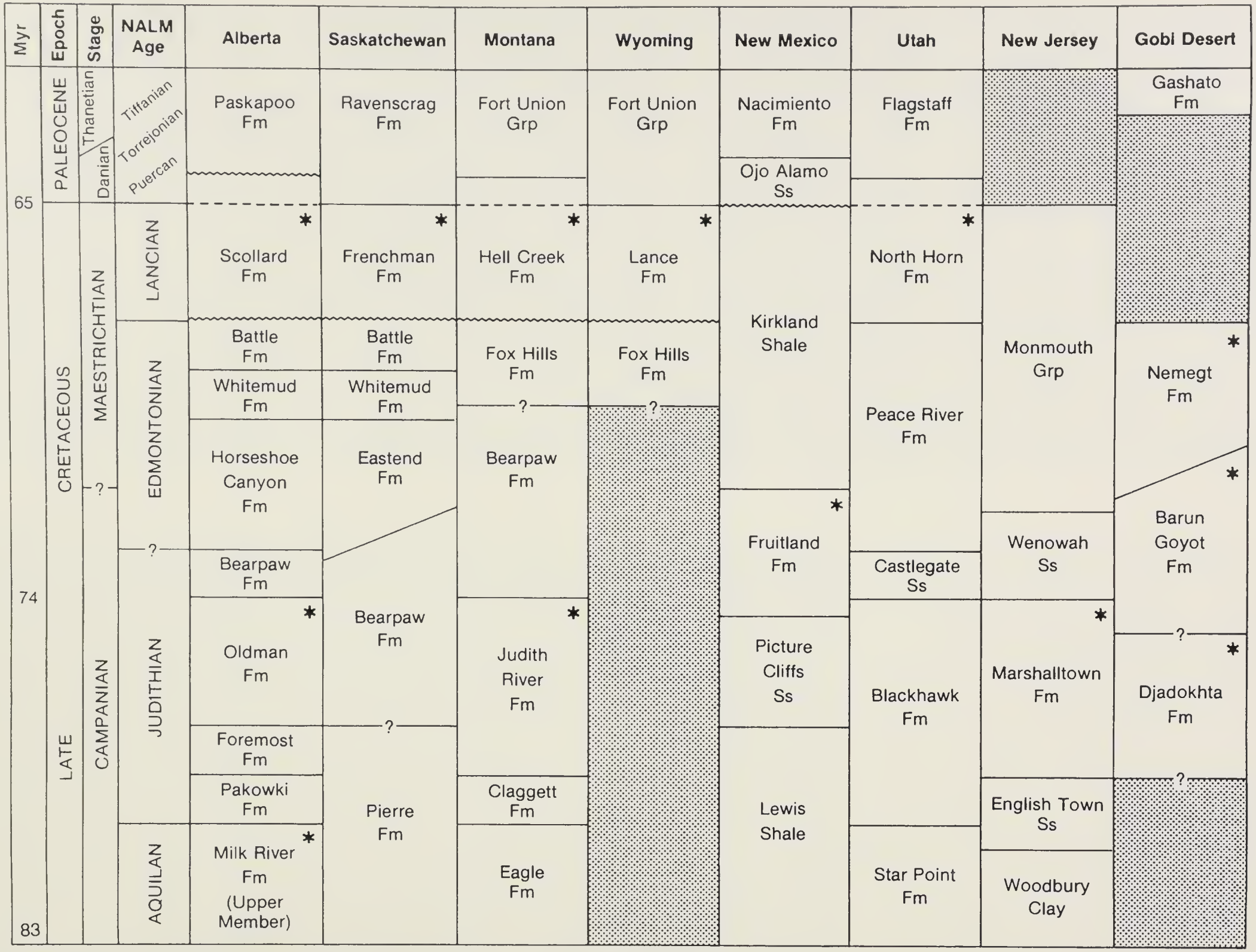

Fig. 3.—Chart showing correlation of the Upper Cretaceous (Campanian–Maastrichtian) lizard fossil-bearing formations (marked with an asterisk) in North America and Asia.

(Dodson, 1983, 1987; Brinkman, 1990; Eberth, 1990*b*) have yielded important results relevant to the sedimentology and the paleoecology of the formations.

Gilmore (1932) named *Polyodontosaurus grandis,* a supposed lizard, on the basis of a small dentary (NMC 8540) from the Belly River Formation (= Oldman and Foremost formations, see Lerbekmo, 1989); but later work by C. M. Sternberg (1951) and D. A. Russell (1969) indicated that the specimen actually belongs to a troodontid dinosaur. D. A. Russell (1969) regarded *Polyodontosaurus grandis* as a synonym of *Stenonychosaurus inequalis,* which is now commonly agreed to be a synonym of *Troodon formosus* Leidy, 1856 (see Currie, 1987; D. A. Russell, 1989; Osmólska and Barsbold, 1990).

The Wapiti Formation (Dawson, 1881) in northwestern Alberta may include nonmarine deposits that are younger than the Oldman Formation (Allan and Carr, 1946; Langston, 1965). C. M. Sternberg (1951) described a lizard (*Chamops* cf. [*C.*] *segnis*) from member B of the Wapiti Formation, Kleskun Hills, near Grande Prairie. The age of the formation ranges from Campanian to Maastrichtian (Stott, 1975), whereas member B of the formation is probably late Campanian or somewhat younger in age. Recent discovery of the ceratopsian *Pachyrhinosaurus* in the same formation at Pipestone Creek by RTMP field parties may indicate that at least part of the formation is equivalent to the Horseshoe Canyon Formation of central Alberta, and hence is Edmontonian in age (Tanke, 1988; Dodson and Currie, 1990).

Lance Formation and Equivalents.—The Lance Formation in Wyoming and its equivalent Hell Creek Formation in Montana are somewhat outside the region for this study, and the lizard fossils from these formations have been previously described by various authors (e.g., Marsh, 1892; Gilmore, 1928; Estes, 1964, 1969*b,* 1983*a*; and Estes et al., 1969). However, new specimens collected by UALVP field parties during the 1969–1976 period yield new information requiring a review of certain known taxa, and more importantly provide the specimens for recognition of several new taxa, which are closely related to those in the study area; therefore, these specimens are also included in this paper.

Exposed mostly in the Powder River Basin of eastern Wyoming, the Lance Formation consists of a succession of interbedded siltstones, channel sandstones, shales, and lignites (Clemens, 1960, 1963; Estes, 1964). The earliest discovery of vertebrate fossils from this formation was reported by Marsh (1889), who referred to the deposits as the "Ceratops beds." Since then, a series of names has been used for the deposits ("Lance Creek beds," "Converse County beds," "Laramie beds," and "Lower Fort Union"; for earlier citations, see Clemens, 1963; Estes, 1964) until Stanton (1910), who named the unit as the Lance Formation. The formation is overlain by the Fort Union Formation or Group and underlain by the brackish water sediments of the Fox Hills Formation. The maximum thickness of the formation is about 750 m in the type area (Clemens, 1963). The lizard fossils previously reported from this formation represent about 13 species in 13 genera (Estes et al., 1969; Estes, 1983*a*).

The Hell Creek Formation consists of nonmarine deposits overlying the Fox Hills Formation (brackish water deposits) in eastern Montana. The formation is composed mainly of gray to brown sandstones and shales (L. S. Russell, 1964) of fluvial origin (Fastovsky, 1987). The maximum thickness of the formation is about 100 m along Hell Creek (Brown, 1907), but varies in adjacent areas (Archibald, 1982). The Bug Creek Anthills (BCA) and nearby localities in the Hell Creek Formation have yielded a vertebrate fauna (Sloan and Van Valen, 1965; Estes et al., 1969; Estes and Berberian, 1970) that has figured importantly in recent debates concerning the events at the K–T boundary in North America and the timing of aspects of mammalian evolution. As Archibald (1982) pointed out, the major argument centers on the age of the fauna: whether the BCA fauna is younger than or essentially contemporaneous with the Lancian fauna. Estes et al. (1969) and Estes and Berberian (1970) stressed the overall similarities in the components of the two faunas, suggesting the "time of deposition of the upper parts of both the Lance Formation and the Hell Creek Formation was essentially synchronous" (Estes and Berberian, 1970:9), whereas Archibald (1987*a,* 1987*b*) and Sloan (1987) proposed a Bugcreekian Age (Stage) in recognizing the age of the BCA local fauna as younger than Lancian. Since the evidence is not decisive, the latter proposal has not been widely accepted, although the uppermost parts of the Hell Creek Formation otherwise include Paleocene deposits (Archibald, 1982).

In central Alberta, Lancian rocks are called the Scollard Formation, formerly "the upper part of the Edmonton Formation," "the Upper Edmonton Formation" (see Lillegraven, 1969), or "the Scollard Member" of the Paskapoo Formation (Irish, 1970). The Scollard Formation, as Gibson (1977) defined

it, includes Paleocene deposits at its top. Lithologically, the formation "consists of an interbedded, interfingering sequence of argillaceous sandstone, siltstone, mudstone, and shale. Minor amounts of coal (Seams Nos. 13–14), bentonite, and tuff occur in the formation" (Gibson, 1977:7). The maximum thickness of the formation is about 85 m in the Huxley–Big Valley area (Gibson, 1977), and Coal Seam No. 14 (Paleocene part, about 18 m above the K–T boundary) has recently yielded a radiometric date of 63 Myr (Lerbekmo and Coulter, 1985). The Scollard Formation rests unconformably on the Battle Formation, which contains a layer of volcanic depositon called the Kneehills Tuff, dated as 65–66 Myr (Folinsbee et al., 1965; also see Lerbekmo and Coulter, 1985). Fossil lizards were previously unknown from the Scollard Formation, although a rich mammalian fauna from several localities along the Red Deer River valley has been reported and described (see Clemens and Russell, 1965; Lillegraven, 1969).

In southwestern Saskatchewan, the northward extension of the Hell Creek Formation of eastern Montana is called the Frenchman Formation, which was previously known as the "lower Ravenscrag" (see Russell and Landes, 1940; Furnival, 1946; Johnston and Fox, 1984). The formation is mainly composed of coarse-grained greenish-brown sandstones, silty sandstones, and shales (Furnival, 1946), and rests on the Battle and Whitemud formations at an unconformable contact. The maximum thickness of the formation is about 100 m (L. S. Russell, 1964), representing the terrestrial sediments of the last 1.5 Myr of Late Cretaceous time (Lerbekmo, 1987). The earliest discovery of lizards from the Frenchman Formation occurred in 1921 by C. M. Sternberg (see Gilmore, 1928:18; GSC 2912, a caudal vertebra, originally cited as from the Lance Formation, Rocky Creek, Saskatchewan). Later reports of vertebrate fossils from the formation were made by L. S. Russell (1964), Fox (1989), Tokaryk and James (1989), and Storer (1991).

DENTAL MORPHOLOGY AND TERMINOLOGY

In this section, we define dental terms used subsequently and explain their use as appropriate, noting ambiguities and even errors in the previous literature on lizard tooth morphology, including the use of mammalian nomenclature for the dental anatomy of lizards.

Tooth Form and Implantation

It is common in lizards that the primitive reptilian homodont dentition has been modified by a differentiation of the marginal teeth, resulting in some degree of heterodonty. The anterior teeth of some lizards are enlarged and canine-like, and the lateral or cheek teeth may be conical, bicuspid, tricuspid, multicuspid, crested, or even enlarged to form crushing plates. Estes and Williams (1984) have compiled data on the development of heterodonty in various groups of lizards.

The evolution of heterodonty in lizards is associated largely with the variety of feeding habits and different dietary demands. For example, the combination of sharp anterior conical teeth with bicuspid or tricuspid cheek teeth seems best adapted for capturing and eating insects with chitinous exoskeletons (Hotton, 1955); while blunt anterior conical teeth combined with enlarged posterior crushing teeth seems designed for feeding on hard-shelled beetles or even molluscs (Conant, 1955). Except for the acrodont dentition of adults in agamids and chamaeleonids, the marginal teeth of most lizards are replaced a number of times during their life history (see, e.g., Edmund, 1969). Thus, the teeth of most lizards are polyphyodont. However, some teiids show replacement suppression as adults (MacLean, 1974).

It is generally considered that there are basically three types of tooth attachment in reptiles; namely, acrodont, in which the tooth is ankylosed to the summit of the jaw (also see discussion in Gauthier et al., 1988; Estes et al., 1988); pleurodont, in which the tooth is attached to the inner surface of the lateral wall of the jaw; and thecodont, in which the tooth root is sheathed in a deep socket in the jaw. However, as Romer (1956) has pointed out, the distinctions between these classic types have tended to break down owing to increasing knowledge of fossil and living reptiles. Besides the three terms above, at least the following have been used in the literature to describe intergrades between the basic types of tooth implantation: protothecodont, subthecodont (Camp, 1923; Edmund, 1969; Evans, 1990); subacrodont (Estes, 1964), hyperacrodont (Camp, 1923; Malan, 1963), pseudoacrodont (Sulimski, 1978); subpleurodont (Estes, 1964), pleurothecodont (Gilmore, 1928); ankylothecodont (Chatterjee, 1974; Benton, 1983). These terms have certainly enriched

our vocabularies in the recognition of intermediate conditions between the three classic types of tooth attachment, but they also cause confusion.

Using different terms for the same mode of tooth attachment results in ambiguities, since the differences between "protothecodont" and "subthecodont," "subpleurodont" and "pleurothecodont," and "subacrodont," "pseudoacrodont," and "hyperacrodont" are indistinguishable. We prefer to use four of these terms as supplementary terms for the intergrades between the three classic types of tooth implantation. Specifically, protothecodont is appropriate for the condition in some early (stem) reptiles, such as cotylosaurs; subthecodont for some diapsids, such as choristoderes; subpleurodont (sensu Estes, 1964) for the condition between pleurodont and subacrodont, as is commonly seen in teiids; and subacrodont for certain aberrant teiids, such as *Haptosphenus* (Estes, 1964) and *Adamisaurus* (Sulimski, 1978). Another term, ankylothecodont, has been clearly defined for the specialized tooth implantation seen in rhynchosaurs, in which the marginal teeth are fused in the sockets as a combination of acrodonty and thecodonty. This type of tooth attachment is unknown in any lizards. Vorobyeva and Chugunova (1986) use "hyperpleurodontal attachment" with respect to the dentition of geckos, a condition termed as pleurodont by most other authors.

Using the same term for different conditions of tooth attachment also engenders confusion. For example, Camp (1923) used the term "hyperacrodont" for the pattern in *Sphenodon,* Agamidae, and Chamaeleonidae (a mode of implantation now commonly termed acrodont), while Malan (1963) used the same term "hyperacrodont" to describe the condition seen in *Howesia,* a South African rhynchosaur, which is more appropriately termed ankylothecodont (Chatterjee, 1974; Benton, 1983). Another example is that of Camp (1923), who used the term "subthecodont" for *Chamops* (more appropriately termed subpleurodont by Estes in 1964), while the term "subthecodont" has been used more recently as a substitute for "protothecodont" in most stem reptiles (see Edmund, 1969) and in some diapsids (see Evans, 1990).

Terms Used in Text

In this study, technical terms for osteological and dental features of lizards are adopted, for the most part, from previous authors, including Goodrich (1930), Estes (1964, 1983*a*), Romer (1956), Edmund (1969), and Estes et al. (1988). Since some terms are not commonly used in the description of fossil reptiles other than lizards, it is necessary to define them explicitly as follows:

Inferior alveolar foramina: external mental foramina in the lower jaw through which pass fibers of the inferior alveolar branch of cranial nerve V_3 (Estes, 1964; Northcutt, 1979).

Interior alveolar canal: a canal for blood vessels and nerves supplying the teeth and lateral surface of the jaws; includes the superior alveolar canal in the maxillary and the inferior alveolar canal in the dentary (Estes, 1964; Northcutt, 1979).

Interior alveolar foramen: internal opening of the superior or inferior alveolar canal within the upper or lower jaws, including an anterior interior alveolar foramen and a posterior interior alveolar foramen (Estes, 1964).

Internal Meckelian foramina: internal mandibular foramina (Goodrich, 1930), including anterior Meckelian foramen, anterior alveolar foramen, anterior mylohyoid foramen, and the posterior mandibular foramen (fossa) in the lower jaw, for the passage of mandibular nerve branches and blood vessels supplying the floor of the mouth and the tongue (Romer, 1956).

Intramandibular septum: a partition posteriorly located in the Meckelian canal, functioning in separating Meckel's cartilage from the lateral nerves and blood vessels (Estes, 1964; Estes et al., 1988).

Subacrodont: attachment of the marginal teeth mostly to the jaw summit, but also to the remaining lateral parapet, which is one-third or less of the tooth height (see Gao and Fox, 1991); this condition is usually associated with loss of the sulcus dentalis.

Subdental shelf: a shelf-like medial extension of the dentary below the tooth row (Estes et al., 1988), often contributing to the sulcus dentalis and the spleniodentary articulation in the lower jaw. The shelf may carry a subdental ridge in some scincomorphans.

Subpleurodont: attachment of the marginal teeth to the medial surface of the lateral parapet of the jaw, which remains low, between one-half and one-third of tooth height (Estes, 1964).

Superior alveolar foramina (= maxillary foramina; du Bois, 1943): superior labial foramina on the maxillary, through which pass fibers of the superior alveolar branch of cranial nerve V_2.

Supradental shelf: a shelf-like medial extension of the maxillary above the tooth row, often bearing an anterior vomerine process and a posterior palatine process; when a sharp ridge is developed on

the shelf, it is termed the supradental ridge (Estes, 1964).

Sulcus dentalis: dental gutter separating the tooth bases from the supradental ridge of the maxillary and from the subdental ridge of the dentary (Estes, 1964).

Terms Unsuitable for Dental Description in Lizards

Certain terms have been used inappropriately in the literature on the dental morphology of lizards. The relevant publications are scattered; the terms listed below are only those that we have encountered in an incomplete survey of the literature.

"Triconodont" and "Symmetrodont".—Some authors (Camp, 1923; Gilmore, 1928; Twente, 1952; Savage, 1963; Presch, 1970, 1974*a*, 1974*b*; Estes, 1983*a*; Estes and Williams, 1984; Winkler et al., 1990) apply the terms "triconodont," "trilobate" (Camp, 1923), "tritubercular," or "symmetrodont" when referring to lizard teeth having three cusps. Contrary to Estes and Williams (1984), who favor the term "triconodont," we strongly suggest using "tricuspid" to replace this and other terms applied to teeth having three cusps. "Triconodont," "symmetrodont," and "tritubercular" are terms that have been used conventionally as the basis for taxonomic names for certain groups of fossil mammals or as descriptive terms for mammalian dentitions, so that use of these terms for lizards is inappropriate and can render only confusion. "Trilobate" is so close in spelling to *Trilobites* (the synonym of *Janassa*, a chondrichthyan fish, see Romer, 1966:351) and "trilobites" (a group of arthropod invertebrates) that use of this term for lizards should be avoided in order to designate clearly the dentition of lizards. Similarly, "bicuspid" is considered to be a better term than "biconodont" for those teeth having two cusps.

"Molar" and "Molar Hypertrophy".—"Molars" are the unreplaced postcanine teeth of mammals (Romer, 1966:191); therefore, this term is best restricted to mammals, and should not be used for other vertebrates, even for the ancestral stock of mammals (mammal-like reptiles). Smith (1946:7) stated that "in the Agamidae the tooth modification is carried still further, to such a point that molars, incisors, and canines may be distinguished; the parallelism with the mammalian condition is emphasized by the fact that the molars are not replaceable whereas the other teeth are." This statement is incorrect in its use of mammalian terminology: some agamids indeed develop anterior, enlarged, canine-like teeth (but not the canine as defined in mammals, as teeth situated between the lateral incisors and the first premolar), and posterior cheek teeth that are not replaced because they are acrodont. There is no differentiation of incisors, canines, premolars, and molars in lizards, although some lizards are heterodont; for example, some teiids display a combination of canine-like anterior teeth and enlarged, crushing cheek teeth (see Estes and Williams, 1984). These teeth are better termed canine-like (caniniform) and molar-like (molariform), rather than canines and molars. Similar use of terms as Smith's is seen in Gilmore (1943*a*: "incisors," "canines," and "last molar"), Harris (1963, 1964: "incisor of rainbow lizard"), and Estes and Williams (1984: "molar hypertrophy" and "molar expansion"). Applying these terms to the dentition of lizards is incorrect and should be avoided.

"Dental Formula".—Some authors (Gilmore, 1926, 1928, 1942*b*; Presch, 1970, 1974*b*; Sulimski, 1975) inappropriately refer to a dental formula in systematic descriptions, or even diagnoses, of lizard taxa. A dental formula is the formula that expresses mammalian heterodonty; that is, the numbers of each category of teeth for a given taxon of mammals (Barghusen and Hopson, 1979; Carroll, 1988). Accordingly, a dental formula is used for mammals because, generally speaking, both tooth number and tooth form for a mammalian species are invariably stable, with a fixed number of tooth types (e.g., incisors, canines) and a fixed number of positions or loci for each type along the tooth row. The lizard dentition is not the same. Since the marginal teeth of lizards are not differentiated into incisors, canines, premolars, and molars, use of a dental formula for lizards is inappropriate.

Furthermore, the dentition of lizards is not static ontogenetically as in mammals: owing to rapid (and sometimes irregular) tooth replacement along with ontogenetic changes in the length of tooth row, the number of marginal teeth in lizards is individually variable in the same species. Ray (1965) and Greer (1991) pointed out that the number of tooth positions in lizards is correlated largely with size, and size is mainly an ontogenetic or sex character. Edmund (1969:tables I–VIII) demonstrated that tooth number is quite variable in different individuals of the same species (e.g., dentary teeth of *Iguana iguana* vary from 17 to 29, depending on differences of size and age). MacLean (1974) provided comparable data for dentary tooth counts in gymnophthalmids (*Ptychoglossus*, 15–35; *Alopoglossus*, 18–32; *Placosoma*, 17–18; *Argalia*, 18—19). Thus, tooth

count alone is nondiagnostic for lizard taxa in most cases. However, in combination with tooth form and other characters, tooth count is broadly useful in comparison of closely related species of lizards. Nevertheless, unless the ontogenetic change is well understood, using tooth count to diagnose lizard taxa should normally be avoided.

SYSTEMATIC PALEONTOLOGY

Class Reptilia Linnaeus, 1758
Subclass Diapsida Osborn, 1903
Infraclass Lepidosauromorpha Benton, 1983
Superorder Lepidosauria Haeckel, 1866
Order Squamata Oppel, 1811
Suborder Lacertilia Owen, 1842

The suborder "Lacertilia" is a paraphyletic group by cladistic definition as it includes lizards but not amphisbaenians and snakes, which are highly specialized squamates sharing a common ancestor with lizards. Because of the cladistic paraphyly of the "Lacertilia," several authors (Estes et al., 1988; Rieppel, 1988; Estes, 1991) recommend abandonment of this name. The term "Sauria" is used as a synonym of "Lacertilia" by some authors (e.g., Evans, 1988; Rieppel, 1988), but is defined by others (e.g., Gauthier et al., 1988; Laurin, 1991) in a very different way, as a higher taxon including both Lepidosauromorpha and Archosauromorpha. "Lacertilia" is retained in this paper as a taxonomic term for "lizards" as traditionally employed (see, e.g., Camp, 1923; Romer, 1956; Robinson, 1967; Carroll, 1988), since consensus on squamate classification has not been achieved. There have been suggestions (Estes et al., 1988; Rieppel, 1988; Estes, 1991) to classify Iguania and Scleroglossa (noniguanian squamates including amphisbaenians and snakes) as equal taxa; however, the higher classification of squamates is beyond the scope of this paper and is not considered further here.

Infraorder Iguania Cuvier, 1807
Family Iguanidae* Gray, 1827

The family Iguanidae* is a large group, containing more than 600 species in some 60 genera (e.g., Frost and Etheridge, 1989). Cladistically, the family is a metataxon indicated by an asterisk (Gauthier et al., 1988; Archibald, 1994: ambitaxon), which can only be defined provisionally as primitive iguanians that lack acrodontan synapomorphies (Estes et al., 1988). To clarify the phylogenetic status of the group, a thorough study of the interrelationships of its former subfamilies or subgroups is needed badly (an attempt was made by Frost and Etheridge, 1989).

Extant iguanids are largely New World (including the West Indies and Galápagos) in distribution, with the exception of three genera that occur in Madagascar, and in Fiji and the Tonga Islands, respectively; they do not inhabit Eurasia, Africa, and Australia. Such a puzzling distribution has been known as "one of the paradoxes in classic biogeography," and "a biogeographic enigma" (Blanc, 1982). Both the classic view (e.g., Darlington, 1957) and the current South American origin hypothesis (see, e.g., Estes and Price, 1973; Cracraft, 1973; Blanc, 1982; Estes, 1983*b*) suggested a southern continent origin for the Iguanidae*; however, more recent discoveries of Late Cretaceous fossils of the group from Spain (see Astibia et al., 1990), the Gobi Desert (Borsuk-Bialynicka and Alifanov, 1991; Gao and Hou, 1992, 1995), and North America (this paper) argue for a possible northern continent origin of the group.

Genus *Cnephasaurus*, **new genus**

Etymology.—*knephas* + *sauros* (Greek, masculine), meaning "twilight lizard"; this lizard may have been active at twilight hunting for grasshoppers, by analogy with its presumed relative, extant *Crotaphytus*.

Type and Only Known Species.—*Cnephasaurus locustivorus*, new species.

Range.—Upper Cretaceous, North America.

Diagnosis.—As for the type and only known species.

Cnephasaurus locustivorus, **new species**
(Fig. 4, 5A–C)

Etymology.—*locusta* + *voro* (Latin), meaning "grasshopper-eating"; the diet of this lizard may have consisted largely of grasshoppers, judging from its dentition.

Holotype.—UALVP 29921, a right maxillary having 11 well-preserved teeth and broken bases of three others.

Type Locality and Horizon.—MR-6 locality, Verdigris Coulee, approximately 30 km east of the village of Milk River, southern Alberta; upper member of the Milk River Formation (Aquilan), Upper Cretaceous.

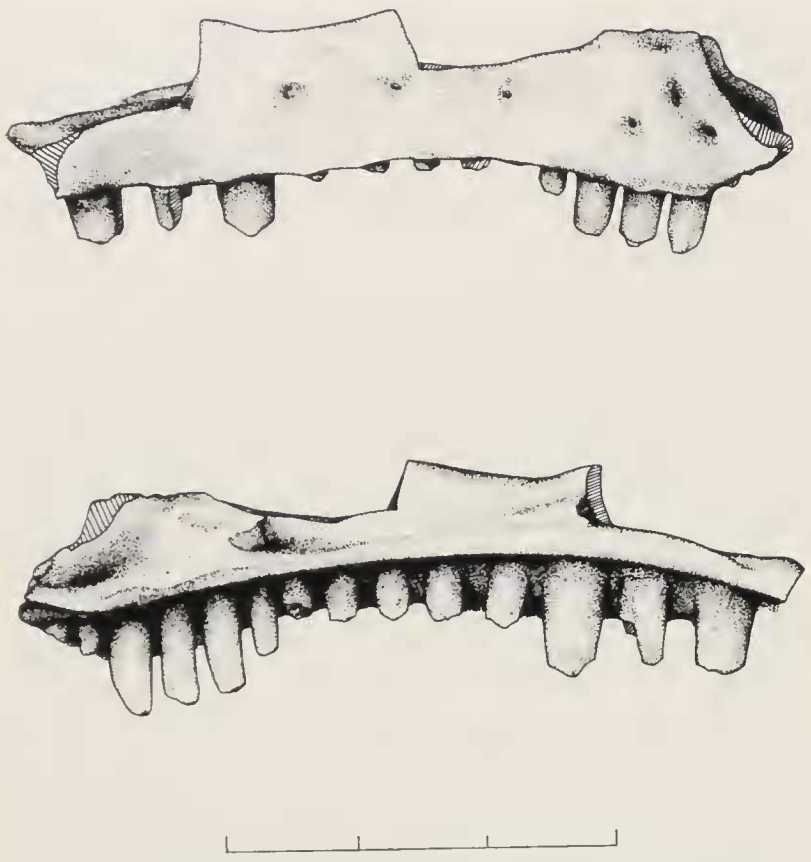

Fig. 4.—*Cnephasaurus locustivorus,* new genus and species, Milk River Formation, Alberta: UALVP 29921 (holotype), incomplete right maxillary, lateral (above) and medial (below) views. Scale = 3 mm.

Referred Specimen.—UALVP 33386, topotypic left maxillary with four teeth and broken bases of two others.

Known Distribution.—Known only from the type locality and horizon.

Diagnosis.—An early Campanian small iguanid, closely resembling extant *Crotaphytus* Holbrook, 1843 in having a highly heterodont dentition, but differing from the latter as follows: premaxillary process much shorter; nasal process unretracted; palatal process on supradental shelf lacking; posterior interior alveolar foramen retaining position close to posterior end of tooth row.

Description.—The holotype maxillary (UALVP 29921, Fig. 4, 5A, B) is small and delicately built, having a total length of about 6 mm. The specimen is anteriorly nearly complete, but broken dorsally and posteriorly; the nasal process (dorsal process or facial process of authors) is missing and the tooth row is incomplete. Anteriorly, both the lateral and the medial premaxillary processes are short and delicate, and not clearly divergent from each other. The anterior interior alveolar foramen is as small as the lateral superior alveolar foramina, and opens anteriorly above the base of the premaxillary processes.

Medially, the holotype bears a slender but clearly defined supradental shelf, the medial border of which is straight in dorsal view, owing to the lack of a palatal process. No definite supradental gutter can be recognized. Anteriorly above the supradental shelf (at the level of the sixth tooth position) is a small pocket-like notch that probably received the lateral process of the palatine. Posteriorly, a relatively large posterior interior alveolar foramen opens above the 12th tooth position. This condition is different from that in *Crotaphytus,* in which the foramen is shifted to a more anterior position, close behind the anterior interior alveolar foramen.

UALVP 29921 has 14 tooth positions preserved, including 11 teeth and the broken bases of three others. With probably the two posteriormost teeth missing, a complete count is estimated at about 16. The maxillary tooth row is strongly heterodont: the first two teeth are broken, but were apparently slender and procumbent; the following three are clearly cylindrical and unicuspid; the sixth tooth is much reduced in size but still remains unicuspid and as cylindrical as the more anterior teeth. This tooth is followed by five even shorter and stouter middle teeth, the crowns of which are laterally compressed and medially concave. Behind these are three posterior teeth, which are strongly enlarged. Both the middle and posterior teeth are broadly based and tricuspid (or incipiently tricuspid), but the posterior ones are much larger and more robust, and separated from the smaller middle ones by an abrupt increase in size along the tooth row. Corresponding to the heterodonty of the maxillary teeth, the spacing between the tooth positions is also variable along the tooth row: the anterior unicuspid teeth are closely spaced and the middle and posterior tricuspid teeth are more widely spaced from one another. These teeth are pleurodont, with half or more than half of their height attached to the lateral parapet of the jaw. No replacement pits can be seen in this specimen.

The lateral surface of the maxillary is smooth, with no osteodermal incrustation. Six superior alveolar foramina, all small and rounded, are spaced equally except for the anteriormost two, which are closer together. The posteriormost foramen, which is usually associated with the posterior interior alveolar foramen, is located close to the posterior end of the maxillary, in this respect differing from that in *Crotaphytus,* in which the foramen is located lateral to the nasal process and anterior to the midpoint of the tooth row. The nasal process of the maxillary is mostly broken off, but the dorsal border posterior to the nasal process indicates that the nasal process probably descended sharply anterior to the midpoint of the tooth row; therefore, the nasal process is located anteriorly in front of the midpoint of the tooth row. An incomplete survey of this character state among extant lizards indicates that this condition is probably unique to iguanians within the Squamata.

Discussion.—The new genus and species *Cnephasaurus locustivorus* is based principally on a small maxillary, UALVP 29921, which is designated as the holotype. In addition, UALVP 33386 (Fig. 5C), a topotypic maxillary fragment of similar size and having the same tooth form, is referrable to the same species. This new lizard from the upper member of the Milk River Formation is classified in the family Iguanidae* on the basis of its close resemblance in dentition to extant *Crotaphytus.*

Perhaps the most unusual characteristic of this lizard is the regional differentiation of the tooth form accompanied by a sharp change of tooth size. As described above, the tooth row of this species consists of six slender, high-crowned, unicuspid anterior teeth, followed by five or so "pygmy" and incipiently tricuspid middle teeth, and then the en-

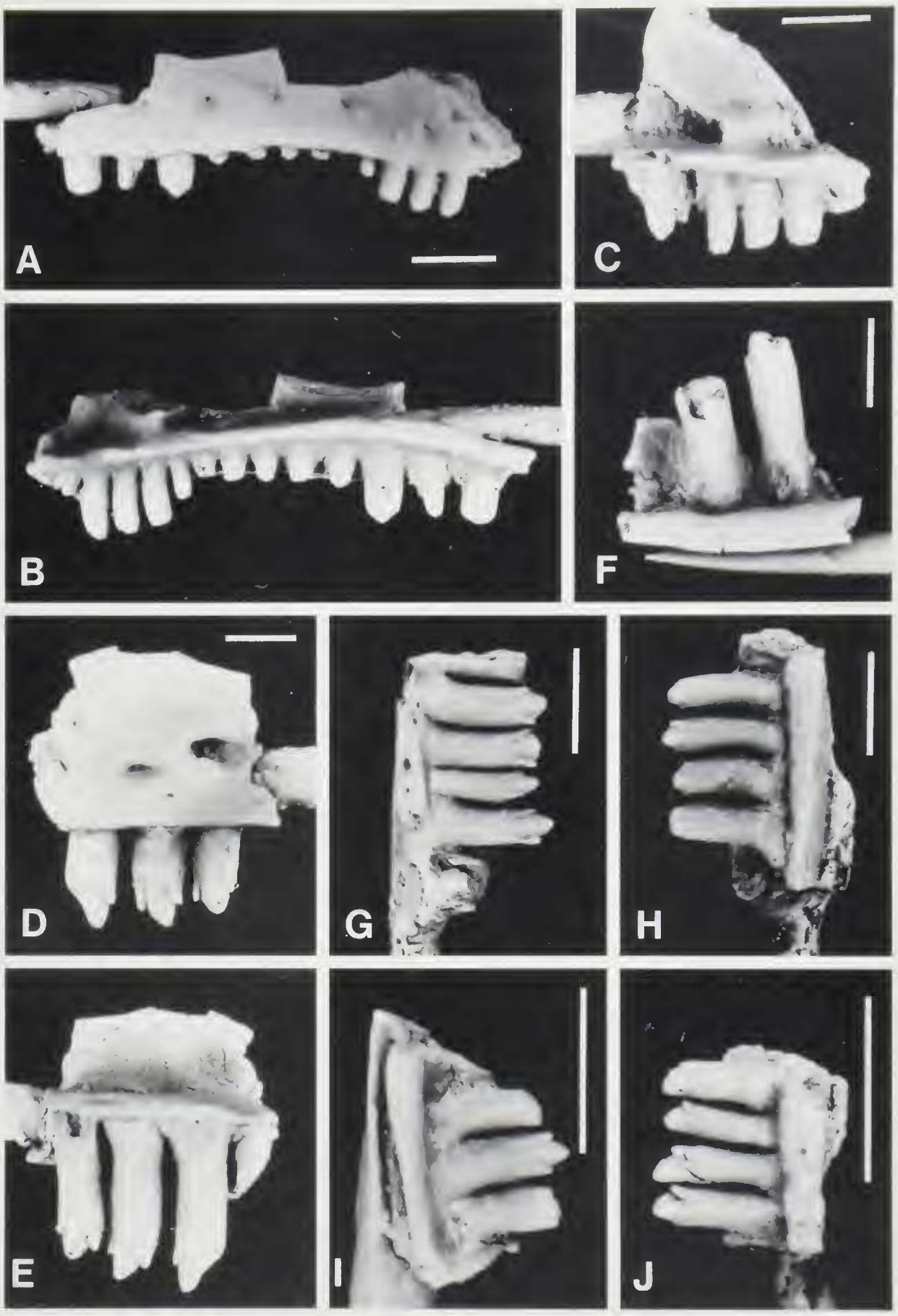

Fig. 5.—*Cnephasaurus locustivorus,* new genus and species, Milk River Formation, Alberta: A, B, UALVP 29921 (holotype), incomplete right maxillary, lateral and medial views; C, UALVP 33386, incomplete left maxillary, medial view. Iguanidae*, new genus and species (A), Milk River Formation, Alberta: D, E, UALVP 29908, left maxillary, lateral and medial views; F, UALVP 29909, left dentary, medial view. Iguanidae*, new genus and species (B), Frenchman Formation, Saskatchewan: G, SMNH P1927.916, left dentary, medial view; H, SMNH P1927.885, left dentary, medial view; I, SMNH P1927.998, right dentary, medial view; J, SMNH P1927.980, left dentary, medial view. Scale = 1 mm.

larged posterior teeth. Both the holotype and referred maxillary have the same pattern of size change with no replacement pits shown on these specimens, suggesting that this pattern of heterodonty is taxonomically significant. An alternative explanation might be that both specimens are from young individuals that have not reached the stage for tooth replacement, and the small size of the middle teeth reflects retarded development at an early postembryonic stage. Nevertheless, since the two specimens show the same condition, the first alternative seems preferable. A similar condition is seen in extant *Crotaphytus,* the dentition of which, according to Hotton (1955), is adapted for feeding on highly active grasshoppers having an integument of intermediate weight. Although the homology of this similarity cannot be tested at present, *Crotaphytus* is indeed the only group that shows this feature. This similarity may indicate a close affinity of the new Milk River iguanid to Crotaphytinae Smith and Brodie, 1982. However, this possibility cannot be fully verified until more extensive evidence is found.

Recognition of *Cnephasaurus* as an early iguanid is both taxonomically and biogeographically significant. Taxonomically, this new form documents an early fossil record of the family Iguanidae*, as the Milk River Formation is of early Campanian age (L. S. Russell, 1975; Fox, 1976; Lillegraven and McKenna, 1986; Lillegraven, 1991), some 18 Myr (Harland et al., 1990) earlier than the Maastrichtian *Pristiguana* Estes and Price, 1973 from Brazil. Biogeographically, it marks a rare discovery of Mesozoic iguanids from North America, which was part of the northern landmass during the Cretaceous. It has been suggested that the Iguanidae* originated in South America (e.g., Estes and Price, 1973; Estes, 1983*b*; Estes and Báez, 1985) and did not reach North America until middle Paleocene or early Eocene time (Sullivan, 1982; Estes and Báez, 1985). The new discovery of early Campanian iguanids from North America, coupled with recent discoveries of a slightly younger fossil record of the same group from Spain (Astibia et al., 1990; S. E. Evans, personal communication, 1995) and the Gobi Desert (Borsuk-Bialynicka and Alifanov, 1991; Gao and Hou, 1992, 1995), indicates the presence of iguanids in North America, Europe, and East Asia well before they occurred in South America in the latest Cretaceous or Paleocene (Estes and Price, 1973; de Muizon et al., 1983; Rage, 1991). The early geological age and primitive morphology of these iguanids challenge the notion of a South American origin, and argue for a possible northern continental origin of the family.

Genus and Species New (A)
(Fig. 5D–F)

Specimens.—UALVP 29908, left maxillary fragment with three well-preserved teeth and the base of another; UALVP 29909, left dentary fragment with two teeth and the space for another.

Locality and Horizon.—MR-6 locality, Verdigris Coulee, approximately 30 km east of the village of Milk River, southern Alberta; upper member of the Milk River Formation (Aquilan), Upper Cretaceous.

Description.—UALVP 29908 (Fig. 5D, E) is a left maxillary fragment that is broken both anteriorly and posteriorly. The facial process is largely missing, but the preserved posteroventral part is vertically straight, indicating that the process in this species is high. The posterodorsal edge of the specimen is a natural border (not a broken surface), representing the descent of the maxillary posterior to the facial process. This specimen also shows that the lateral surface of the maxillary is smooth, bearing relatively large superior alveolar foramina (one shown on this specimen).

Medially, UALVP 29908 shows a thin and slender supradental shelf, which has no dental gutter. Dorsal to the shelf is the narrow opening of the posterior interior alveolar foramen. This foramen usually opens at the posterior part of the tooth row, and the inclined dorsal edge above it clearly indicates that the specimen represents the posterior part of the maxillary. UALVP 29908 bears three well-preserved teeth, which are high crowned and pleurodont, with half of their height attached to the lateral parapet of the jaw. The teeth are basically cylindrical, but are concave medially with the crowns slightly bent lingually. The crowns are tricuspid, having a strongly prominent central cusp and much weaker but clearly defined anterior and posterior side cusps. The crowns are slightly twisted, so that the three cusps are aligned at an angle of approximately 45 degrees to the tooth row, and the central cusp is curved posteromedially. The anterior accessory cusp is slightly stronger than the posterior one.

A dentary fragment (UALVP 29909, Fig. 5F) from the same locality has two teeth preserved, one complete and the other with the crown broken off. The central and anterior cusps are similar to those on the maxillary (UALVP 29908), but the tooth lacks a clearly defined posterior cusp, a condition that can be termed either bicuspid or incipiently tricuspid. It seems likely that the differences in the development of these cusps are relevant to tooth position, with the posterior teeth having strongly tricuspid crowns. However, this interpretation cannot be verified until more nearly complete specimens of this species are recovered. Because of the fragmentary nature of the specimens, the possibility of the second specimen representing another species cannot be ruled out.

Discussion.—The new genus and species (A) is recognized principally on UALVP 29908, while the other specimen (UALVP 29909) is referred to the same species with some uncertainty. Although fragmentary, UALVP 29908 clearly shows that at least the middle and posterior teeth of this lizard are definitely tricuspid, with the central cusp being much

higher than the lateral ones, and the crowns twisted at a 45-degree angle to the straight line of the tooth row. This particular cusp pattern, in association with other characters such as crown height and mode of tooth attachment, provides useful information concerning its taxonomic placement at a familial level.

Tricuspid teeth are commonly seen in Teiidae and Iguanidae*, and also occur in some genera of Xantusiidae (Savage, 1963). In tricuspid teeth of teiids, the three cusps are characteristically more or less equal in height, a pattern that is often closely associated with other characters, such as subpleurodonty and a well-developed dental shelf and sulcus dentalis (see Estes, 1964, 1983*a*; Presch, 1970; Gao and Fox, 1991). All of these features are different from the condition seen in UALVP 29908, excluding the possibility of its affinity to the family Teiidae, which is highly diverse in the North American Upper Cretaceous. Two genera of Xantusiidae (*Klauberina* and *Lepidophyma*) are known to have tricuspid teeth (Savage, 1963), but the tricuspid condition in these genera is obviously different from that of iguanids: in xantusiids, the two side cusps are more lingually located than the central cusp ("anterior and posterior cusps on inner surface of teeth"; Savage, 1963:30).

UALVP 29908 has an interesting combination of high-crowned, tricuspid, and highly pleurodont teeth, while lacking a dental gutter. This combination of character states indicates that the specimen is referrable to the family Iguanidae*. The teeth of iguanids are generally high crowned and pleurodont, and with more or less flared crowns that can be either tricuspid or polycuspid (having four or more cusps), with the exception of having simply peg-like teeth in some highly derived groups. The tricuspid condition in the Iguanidae* is commonly characterized by having "a large apical cusp, smaller anterior and posterior cusps, and more or less parallel sides" (Etheridge and de Queiroz, 1988: 297). Recent cladistic analysis of iguanid phylogeny indicates that tricuspid tooth form is a primitive condition in the family Iguanidae* (Etheridge and de Queiroz, 1988). Thus, UALVP 29908 may represent another primitive early iguanid from the Milk River Formation. However, the specimen is too fragmentary to show the nature of the premaxillary and facial processes, making a comparison with Recent specimens impossible.

Genus and Species New (B)
(Fig. 5G–J)

Specimens.—SMNH P1927.916, dentary fragment bearing five teeth and the base of another; SMNH P1927.885, left dentary fragment bearing four teeth and the bases of two others; SMNH P1927.998, right dentary fragment with three teeth and the base of another; SMNH P1927.980, dentary fragment bearing four well-preserved teeth.

Locality and Horizon.—Gryde locality, in Sec. 19, Tp. 4, R 18, W 3, Frenchman Valley, southwestern Saskatchewan; Upper Cretaceous Frenchman Formation (Lancian).

Description.—SMNH P1927.916 (Fig. 5G) is a fragmentary dentary, which is obviously from a small individual, as shown by the size of the specimen. Although fragmentary, the specimen shows that the subdental shelf is poorly defined and has no dental gutter (sulcus dentalis). The lower portion of the jaw fragment is missing, providing no information about the splenial bone, spleniodentary articulation, and the Meckelian canal. The dentary fragment bears five teeth and the base of another. The five teeth are complete or nearly complete; only the last on the specimen is badly broken. These teeth are high crowned and pleurodont, with the lower half of the teeth attached to the lateral parapet of the jaw. The tooth crowns are flared, slightly recurved, and tricuspid, having a highly prominent main cusp and two much lower side cusps. The side cusps are clearly separated from the central main cusp, and each has a vertically running ridge on the medial surface of the crown. The anterior side cusp is slightly stronger than the posterior one on each tooth. The tooth shafts are slenderly cylindrical and are closely packed along the tooth row. The tooth bases are slightly thicker than the shafts and show no sign of tooth replacement on the specimen.

SMNH P1927.885 (Fig. 5H), a left dentary fragment, has four teeth and spaces for two others preserved. The teeth are high crowned, pleurodont, and the cylindrical tooth shafts are slightly curved. The tooth crowns are not well preserved, but apparently tricuspid. The subdental shelf is slightly stronger than on the other three specimens, and it seems to bear a poorly defined sulcus dentalis.

SMNH P1927.998 (Fig. 5I) is the fragment of a small right dentary, which bears three teeth (one complete and the other two with the crowns broken off) and the space for another. The tooth form of this specimen is similar to that of SMNH P1927.916; that is, slender, cylindrical, and tricuspid, and the subdental shelf is weak with no sulcus dentalis. Each of the two teeth with a broken crown has a resorption pit at the medial side of the tooth base. The Meckelian canal is extremely restricted, opening narrowly ventromedially, indicating a greatly reduced splenial. The lateral surface of the jaw fragment is smooth, relatively flat, and bears two mental foramina that are widely separated from each other by four tooth positions.

SMNH P1927.980 (Fig. 5J) is a left dentary fragment bearing four well-preserved teeth. Like SMNH P1927.916, this fragment shows a weakly developed subdental shelf, and high-crowned and pleurodont teeth closely spaced from one another along the tooth row. The tooth shafts are slender, cylindrical, and the crowns are flared and slightly recurved. However, the tooth crowns of this specimen are clearly bicuspid, differing from the tricuspid condition in SMNH P1927.916. Owing to the incompleteness of the two specimens, we are unable to determine whether the difference of the crown pattern is taxonomically significant, or simply that the two specimens are from a different portion of the dentary tooth row. Therefore, its referral with the other three specimens to the same unnamed taxon is tentative.

Discussion.—Whereas the four specimens de-

scribed above are too fragmentary to show the general jaw configuration, the tooth form of these specimens indicates the presence of at least one new genus and species previously unknown from Lancian horizons. However, the new taxon is unnamed in this study because the available specimens are inadequate to show diagnostic features other than tooth form; jaw structure, such as the morphology of the splenial, is important in determining taxonomic position.

Although this new genus and new species remains unnamed (thus no holotype is designated), SMNH P1927.916 is the specimen on which the new taxon is recognized. It clearly shows tall teeth having flared and tricuspid crowns, a poorly defined subdental shelf, and no sulcus dentalis. These are derived character states that in combination strongly indicate the affinity of this lizard to the family Iguanidae*. Within the Iguanidae*, the closest resemblance in terms of tooth morphology of this Lancian form is to *Ctenosaura* (e.g., *C. similis* Gray, 1831, see Ray, 1965:fig. 5), which has a geographical distribution in Mexico and Central America (Estes, 1983*a*). According to Hotton (1955), *C. similis* is chiefly herbivorous, but its diet also includes insects at times.

SMNH P1927.998 is an important specimen as it shows strong evidence of iguanid affinities: the total loss of the sulcus dentalis, greatly reduced splenial as indicated by the extremely narrow Meckelian canal, highly pleurodont dentary teeth with tricuspid crowns, and direct tooth replacement as suggested by the resorption pits at the medial side of the tooth bases. However, we are unable to determine if this specimen can be grouped with P1927.916 and P1927.885 in the same species as the teeth of this jaw fragment are less high crowned and less flared than those of the two specimens mentioned above. We tentatively put them together on the basis of their tricuspid crown pattern, regarding the differences in tooth height as related to regional variation along the tooth row.

SMNH P1927.980 is similar to P1927.916 in having high-crowned, cylindrical teeth with flared crowns, but differs from the latter in having a bicuspid rather than tricuspid crown pattern. It is closely similar to P1927.916 in every aspect but lacks a posterior side cusp on the crowns. At this stage, we are unable to determine whether this difference is taxonomically significant, or simply reflects differences in cusp pattern along the different parts of the tooth row.

From the above discussion, the four specimens from the Upper Cretaceous Frenchman Formation represent at least one (and maybe more than one) new taxon that is referrable to the Iguanidae* based on tooth form and implantation. They are referred to the same unnamed taxon from their general similarity in tooth form and origin from the same locality. SMNH P1927.916 and P1927.885 are clearly the same kind, whereas P1927.980 and P1927.998 seem to resemble less clearly the former two specimens in terms of crown pattern (number of cusps), but cannot be determined to be a separate taxon at the present time.

Infraorder Scincomorpha Camp, 1923
Family Teiidae Gray, 1827 (sensu Estes, 1983*a*; Presch, 1983)

Boulenger (1885) subdivided the Teiidae (sensu lato) into four major groups (I–IV). His group I was later informally known as "macroteiids" and group II as "microteiids" (Ruibal, 1952). MacLean (1974) recognized the two groups as separate subfamilies (Teiinae and Gymnophthalminae). More recently, Estes (1983*a*) and Presch (1983) independently ranked the two groups as families. "Teiidae" (sensu stricto) as used in this paper refers to Boulenger's group I (macroteiids) in the sense of Estes' (1983*a*) and Presch's (1983) definition. In the most recent study of the phylogenetic relationships of the lizard families, Estes et al. (1988) listed 14 synapomorphies for the family Teiidae, among which the following are unambiguous and reliable character states for fossil teiid studies: replacement teeth developing in deep subcircular cavities at tooth bases (Romer, 1956); cementum deposited extensively on tooth bases (Presch, 1974*b*); vomer elongated, approaching pterygoid (Romer, 1956); splenial hypertrophied, extending anteriorly to the symphysis leaving only a small symphyseal foramen (MacLean, 1974). So far, the earliest known fossil record of this family is of Albian age, from the Comanchean of central Texas (Winkler et al., 1990).

Genus *Chamops* Marsh, 1892

Type Species.—*Chamops segnis* Marsh, 1892.
Range.—Upper Cretaceous, North America.
Diagnosis.—As for the type species (see below).

Chamops segnis Marsh, 1892 (emend. Gilmore, 1928; Estes, 1964, 1983*a*)
(Fig. 6, 7A–E)

Holotype.—YUM 1036, a fragmentary left dentary with five well-preserved teeth, from the Lance Formation, Niobrara County, Wyoming. The holo-

type was originally identified by Marsh (1892) as a right maxillary; the identification was erroneous and was later corrected by Estes (1964).

Referred Specimens.—Frenchman Formation, Gryde locality: SMNH P1927.824–825, P1927.831, P1927.876, P1927.882, P1927.899, P1927.966, P1927.969, P1927.993, P2004.86 (total: ten), incomplete maxillaries; P1927.827, P1927.874, P1927.883, P1927.890, P1927.920, P1927.991 (total: six), fragmentary dentaries. Wounded Knee locality: UALVP 29731, incomplete maxillary; UALVP 29728, 29811–29812, fragmentary dentaries. Scollard Formation, KUA-1 locality: UALVP 29841, fragmentary maxillary; KUA-3 locality: UALVP 29842–29843, incomplete dentaries.

Known Distribution.—Upper Cretaceous Lance Formation, eastern Wyoming; Hell Creek Formation, eastern Montana; Scollard Formation, central Alberta; and Frenchman Formation, southwestern Saskatchewan (all Lancian).

*Diagnosis (Revised from Estes, 1983*a*).*—North American Late Cretaceous teiid, differing from other teiids in the following combination of character states: marginal teeth not crowded along tooth row, oval to subcircular in cross dimensions, except at base where moderately transverse, increasingly swollen posteriorly and becoming distinctly barrel-like in shape; dentary and maxillary tooth row weakly heterodont, with relatively tall anterior teeth unicuspid to weakly bicuspid or tricuspid, somewhat recurved towards tip, becoming more strongly tricuspid and erect posteriorly; accessory cusps set off from main cusp by prominent groove lingually, short groove labially.

Description.—More than 20 maxillaries and dentaries collected in the study area can be confidently identified as *Chamops segnis* on the basis of tooth form and jaw structure. The following description is based on several relatively well-preserved specimens in the collections available for this study. In addition to the specimens enumerated above, several maxillaries and dentaries of the same species, but from the Lance and Hell Creek formations, are also included in the study because they show individual variation in certain features of the tooth row. These include: UALVP 29727, 29729, 29813 (maxillaries), and 29814 (dentary) from the BTB locality of the Lance Formation, Wyoming (the BTB locality is assumed to be near the type locality of *C. segnis* ["Lance Creek" in Gilmore (1928)], and hence, the UALVP specimens are considered topotypic); and UALVP 29724–29726, 29730, 29737–29738 (maxillaries), 29721, 29723, and 29815 (dentaries) from the BCA locality, Hell Creek Formation, Montana.

Maxillary. SMNH P2004.86 (Fig. 6, 7A) is the left maxillary of a young individual, judging from its small size (about half size of UCMP 46033, see Estes, 1964:fig. 47). The maxillary has part of its dorsal process broken away; otherwise it is complete. It has a short premaxillary process, behind which the nasal process rises abruptly as a vertical lateral wall, as in UCMP 46033, a maxillary from the Lance Formation (Estes, 1964:fig. 47). Medially, the maxillary bears a well-developed supradental shelf,

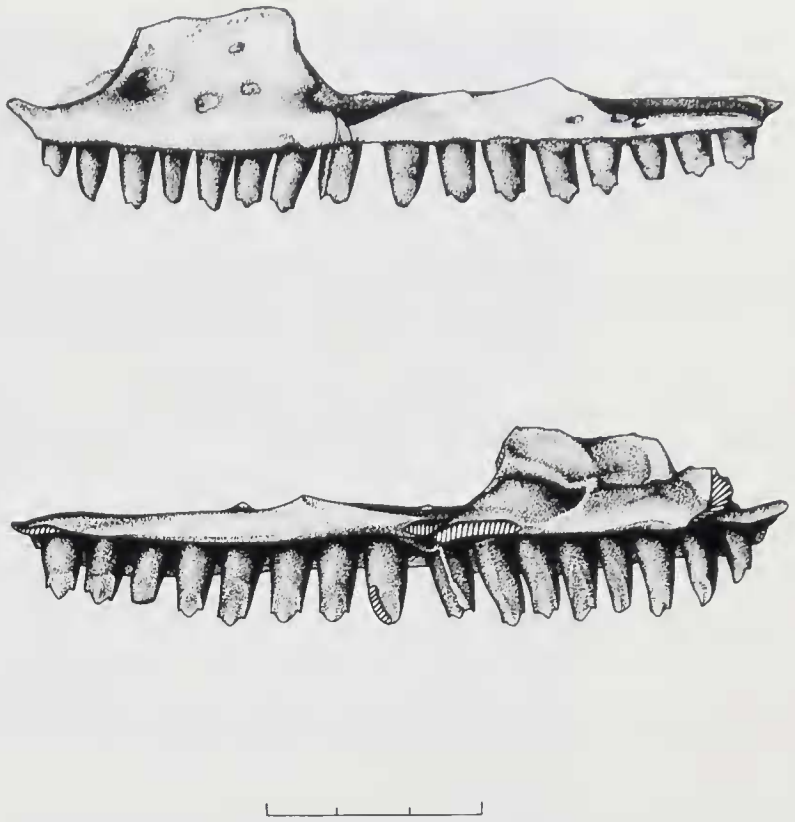

Fig. 6.—*Chamops segnis,* Frenchman Formation, Saskatchewan: SMNH P2004.86, left maxillary, lateral (above) and medial (below) views. Scale = 3 mm.

the medial edge of which is nearly straight, and lacks a palatine process. The posterior interior alveolar foramen opens above the shelf at a position between the fifth and the sixth posteriormost teeth. The full maxillary tooth row is preserved on this specimen and contains 16 short-crowned teeth with swollen shafts. The first four anterior teeth are conical (or weakly bicuspid) and are slightly recurved; the next three are weakly tricuspid, while the rest are broadly tricuspid.

The crown pattern of the maxillary teeth is best shown on SMNH P1927.824 (Fig. 7B), an incomplete left maxillary of the same size as SMNH P2004.86 described above. The specimen has 14 tooth positions (12 teeth and bases of two others), with probably the two anteriormost teeth broken away. In SMNH P1927.824, the tricuspid condition of the maxillary teeth starts from the fifth anterior tooth, and the middle and posterior teeth are short, broadly tricuspid, and slightly concave medially. The third posteriormost tooth on this specimen is medially offset from the tooth row, and the crown is bent laterally; this seems to be the result of pathologic development of the tooth. Tooth implantation is subpleurodont. A shallow sulcus separates the tooth row from the supradental ridge. As in other specimens of the species, the maxillary teeth are moderately spaced from one another, and are slightly concave on the lingual surface. The teeth have a basal deposit of cementum, but it is much less heavy than on larger specimens in the collection. This feature, plus its small size, implies that the maxillary is from a young individual. In comparing smaller and larger maxillaries of *C. segnis* in our collection, the accessory cusps are stronger and better defined in the larger and presumably older individuals, an observation that contrasts with that of Denton and O'Neill (1995) for this species.

Anteriorly, the internal surface of the maxillary of *C. segnis* shows two depressions, one smaller, more anterior and ventral in position, the second and larger one posterodorsal to the first. These depressions probably were associated with soft tissues of

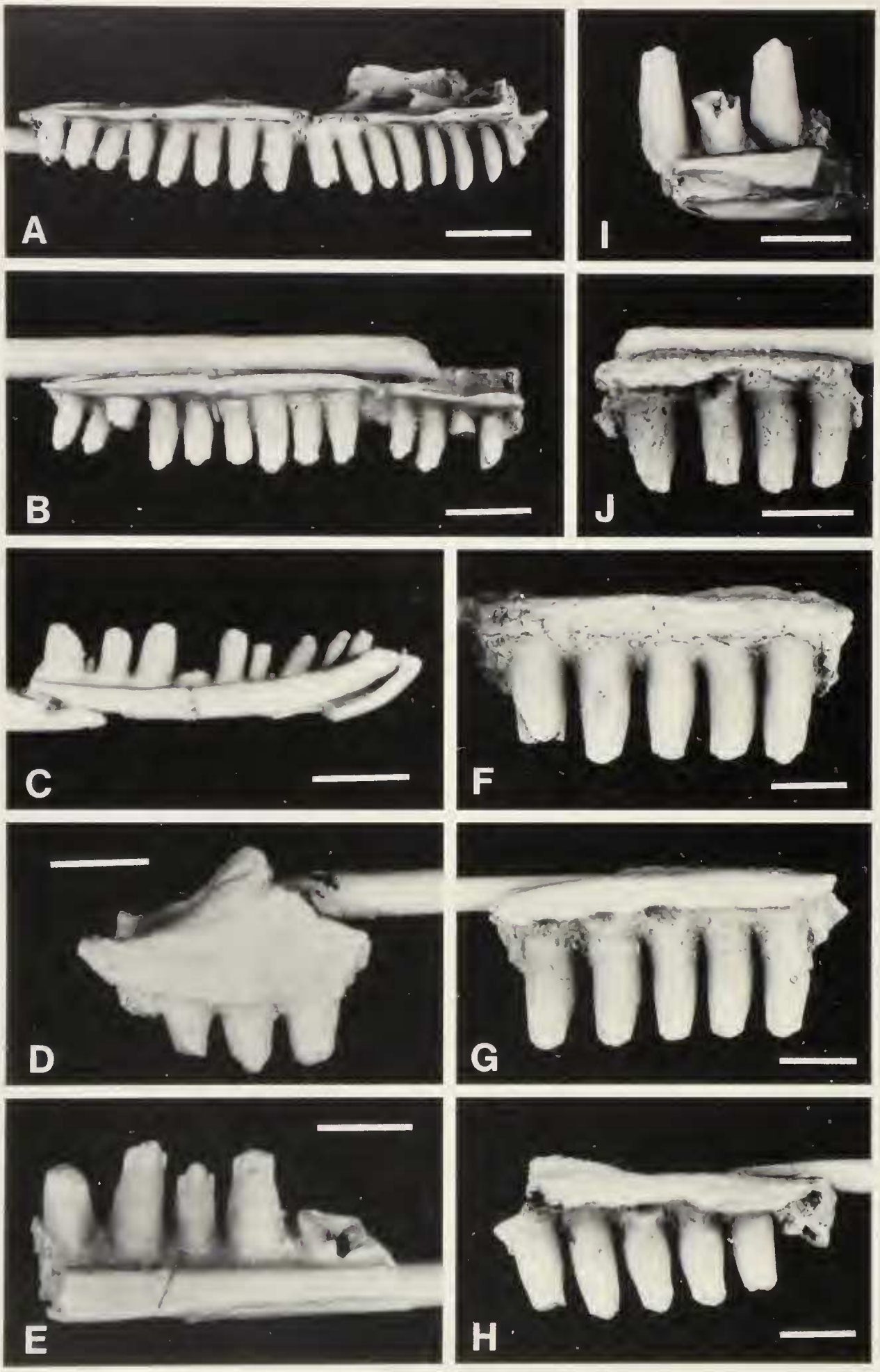

Fig. 7.—*Chamops segnis,* Frenchman Formation, Saskatchewan: A, SMNH P2004.86, left maxillary, medial view; B, SMNH P1927.824, left maxillary, medial view; C, SMNH P1927.874, left dentary, medial view; Scollard Formation, Alberta: D, UALVP 29841, left maxillary, lateral view; E, UALVP 29842, right dentary, medial view. *Chamops* sp., Milk River Formation, Alberta: F, UALVP 29816, left maxillary, medial view; G, UALVP 29826, left maxillary, medial view; H, UALVP 29817, right maxillary, medial view; I, UALVP 29819, right dentary, medial view; J, UALVP 29820, left maxillary, medial view. Seale = 1.5 mm.

Jacobson's organ (Hecht, 1951). The configuration of these depressions in the maxillaries from the Frenchman Formation matches that in the topotypic maxillaries from Wyoming in the UALVP collection, corroborating the identification of these specimens as based on their dental morphology.

Dentary. In this study, 11 dentaries from the Frenchman and Scollard formations are referred to *Champs segnis* on the basis of their tooth form and jaw structure; the best preserved of these is described as follows: SMNH P1927.874 (Fig. 7C), from the Gryde locality of the Frenchman Formation, is an incomplete left dentary bearing 11 tooth positions (eight teeth and the bases of three others). The dentary is from a young individual, as evidenced by its small size. Although most of the lateral wall of the Meckelian canal is broken off, the tooth form and the parts of the dentary that remain provide reliable characters for identification. Medially, the dentary bears a strong subdental shelf, a well-developed sulcus dentalis, and a weak symphyseal surface. The first five teeth are slender, conical, and slightly procumbent; and the remainder of the teeth strongly increase in size posteriorly. Most of these teeth are poorly preserved, but the tricuspid crown pattern is shown at the seventh and the ninth tooth positions. In spite of the small size of the specimen, tooth replacement is shown at the sixth and the tenth positions, where the remaining bases of the replaced teeth still can be seen. In dorsal view, the tooth row is straight, lacking the curvature seen in *Leptochamops* Estes, 1964, another teiid lizard from the same horizon.

Comparison of the specimens from the study area with those from the Lance and Hell Creek formations allows a better understanding of the jaw construction and tooth morphology of this teiid. Generally speaking, the dentary of *Champs segnis* is short and robust, but it has a weak symphysis; it differs from the dentary of *Leptochamops* in having a much wider Meckelian sulcus, much deeper boat-shaped ventral curvature, straight subdental shelf, and a posterior interior alveolar foramen that opens under the 12th tooth position. In addition, the dentary external surface of *Champs* is smoothly convex dorsoventrally, lacking the labial concavity seen in *Leptochamops denticulatus* (Gilmore, 1928).

The tooth row is weakly heterodont: the anterior teeth (four or five) are conical or weakly bicuspid, as shown on the two maxillaries described above and UALVP 29841 (Fig. 7D) from the Scollard Formation; these are followed by a few weakly tricuspid teeth, and then by widely tricuspid posterior teeth with short and swollen shafts. Estes (1964) stated that the incipiently tricuspid anterior teeth are separated from the posterior ones by a "step" (see discussion below), and that the dentary tooth count of *Champs segnis* is 18 on the basis of UCMP 49881, which shows the complete tooth row. Among the specimens used in this study, no dentary contains the full tooth row; the highest number of preserved tooth positions is 11, as shown on SMNH P1927.874 from the Frenchman Formation, Saskatchewan, and the posterior tricuspid teeth are best shown on UALVP 29842 (Fig. 7E) from the Scollard Formation, central Alberta.

The UALVP collections include two specimens of interest from the Oldman Formation that are best considered here. UALVP 33911 is a left maxillary fragment containing four teeth, UALVP 33912 is a right dentary fragment with three complete teeth and a fourth that is broken; both are from the Irvine locality, southeastern Alberta. The teeth on both specimens are tricuspid, with swollen, barrel-like shafts, unique features of the dentition of Lancian *Champs segnis*. Pending the collection of better preserved material, we identify these specimens as *Champs* sp., cf. *C. segnis*; they are readily distinguished from all other teiids known from Judithian horizons.

Denton and O'Neill (1995) cite longitudinal (= vertical) striations of the crown enamel as a synapomorphy uniting *Champs segnis* and their new teiid *Prototeius stageri*. The occurrence of striae on the crown of *C. segnis* is, however, individually variable and, hence, not a characteristic feature of the species, irrespective of its occurrence in *P. stageri*. Similar striations are widespread in scincomorphan lizards and may be primitive for teiids in any case.

Discussion.—Champs segnis was previously known from the Lance Formation, Wyoming (Marsh, 1892; Gilmore, 1928; Estes, 1964, 1983*a*), Hell Creek Formation, Montana (Estes et al., 1969), Frenchman Formation, Saskatchewan (L. S. Russell, 1964; Fox, 1989), and now from the Scollard Formation, Alberta (this paper). There have been other reports of *Champs segnis* from geologically older horizons (for citations see Estes, 1983*a*:95), but a careful review of the fossil evidence indicates that these reports are either unconvincing or based on misidentified specimens (see discussion below). Problems bearing on the taxonomic history, diagnosis, synonyms, and misidentified specimens for this Cretaceous lizard are treated in the following discussion.

Taxonomic History and Relationships of *Champs segnis*. *Champs segnis* was originally named by O. C. Marsh (1892), based on several specimens collected by J. B. Hatcher in 1889 from the Lance Formation, Wyoming. Marsh (1892) designated a left dentary (misidentified as a maxillary) as the type specimen, but provided no specimen number, no description, and no diagnosis for the new genus and species. It was not until 1928, when Gilmore gave a detailed description of Marsh's type specimen and pointed out its diagnostic characters, that *Champs segnis* became a fully established taxonomic name. Gilmore (1928) followed Marsh's incorrect identification and described the type specimen (YUM 1036) as a maxillary. Estes (1964) was the first to note that the type specimen of *Champs segnis* is in fact a dentary. Estes (1964:pl. 2) provided a clear photograph of the type specimen, which shows five (rather than ten) complete dentary teeth and the tooth bases of five others. This condition of the specimen is consistent with Gilmore's (1928:24) description, but different from Marsh's (1892:fig. 2, 3) original figures that show nine complete teeth and the base of another. Therefore, it may be that between 1892 and 1928 the type specimen was damaged, with four teeth broken and lost.

Marsh (1892) offered no opinion regarding the relationships of *Champs segnis*. Subsequently, the

species was referred to the Teiidae by Boulenger (1892) and Nopcsa (1908) without comment, and was placed in the Iguanidae* by Hay (1902), Camp (1923), and Gilmore (1928). Estes (1964:105) noted that "*Champs* differs in many ways from known iguanids, principally in the broadly open Meckelian fossa, the concomitantly large splenial, and less pleurodont implantation of teeth." Recognizing the significant similarities to the extant teiids *Crocodilurus* Spix, 1825 and *Tupinambis* Daudin, 1802, Estes (1964) placed *Champs* in the Teiidae. More recently, Estes (1969*a*, 1983*a*) further recognized that the closest relationship of *Champs* is with *Callopistes* Gravenhorst, 1838, from similarity of maxillary, nasal, quadrate, and parietal bones. The maxillary that Estes used for comparison (UCMP 46033) is restored dorsally from UCMP 46094, and "the parietals and quadrates are referred to *Champs* on the basis of both size and frequency, as well as on their generally teiid appearance" (Estes, 1969*a*:5). New specimens used in this study add no further information as to the reliability of the association of these disarticulated skull elements; however, the relationship of *Champs segnis* to the Teiidae can be determined without reference to skull elements, because teiid synapomorphies are clearly shown on the dentary specimens. These synapomorphies include: (1) large splenial, as indicated by the widely open Meckelian canal; (2) extensive deposit of cementum on the tooth bases; and (3) replacement teeth developing in deep subcircular basal cavities (see Estes et al., 1988, for citations). In addition, other characters, such as the subpleurodont tooth attachment, well-developed subdental shelf, and sulcus dentalis, are consistent with the family Teiidae, and are not found in nonteiids having similar tooth form (e.g., extant *Crotaphytus collaris*).

As Estes (1964, 1969*a*) noted, a character state that *Champs* shares with *Callopistes,* but not with *Crocodilurus* and *Tupinambis,* is the relatively short face. In *Callopistes,* the upper jaw is shorter than one-half of the total length of skull, while it is half, or often longer than half, the length of the skull in other teiids (see Presch, 1970). The short face is also consistent with a higher nasal process of the maxillary in extant teiids (personal observation). Facial elongation is prominent in advanced teiids, such as *Cnemidophorus* Wagler, 1830 and *Ameiva* Meyer, 1795 (MacLean, 1974: "long-snouted species"). Thus, the deep maxillary and short face are probably primitive conditions in teiids (Estes, 1964).

Diagnostic Characters of *Champs segnis*. As mentioned above, Marsh (1892) provided no diagnosis for *Champs segnis* when he named the species. Gilmore (1928:24) was the first to diagnose the lizard as having "teeth pleurothecodont [subpleurodont]; internal and external surfaces of teeth grooved longitudinally; tricuspid; subequal in size; 23 teeth in complete dentary series." However, his count of 23 dentary teeth was based on YUM 1062, a specimen that pertains to another genus and species (*Leptochamops denticulatus*; see Estes, 1964). Actually, the full dentary tooth count of *Champs segnis* is about 18, based on the evidence from UCMP 49881 and UCMP 49871 (see Estes, 1964: fig. 45).

Based on additional collections from the Lance Formation, Estes (1964:102) revised the diagnosis for the species as "a teiid lizard closely related to the living *Crocodilurus lacertinus* and *Tupinambis nigropunctatus,* differing principally from these in the less pronounced heterodonty, and less swollen tooth crowns; if the parietal is correctly referred, this species has a large parietal foramen, unlike all Recent teiids."

More recently, Estes (1983*a*:95) provided the latest version of the revised diagnosis for *Champs segnis*: "teiid lizards apparently with a parietal foramen; tooth row very weakly heterodont, anterior teeth bicuspid or weakly triconodont, separated by an area of reduced tooth size from posterior triconodont teeth that have swollen bases and wrinkled crown surfaces; maxilla deep dorsoventrally; splenial very extensive, almost completely filling the widely open Meckelian sulcus." About this diagnosis, we offer the following comments.

First, the nature of the "area of reduced tooth size" (Estes, 1964: "step") is still unclear; however, it is individually variable within *Champs segnis,* as the change in tooth size is not shown on the holotype (YUM 1036, see Marsh, 1892:fig. 2, 3; Estes, 1964:pl. 2) nor on various other specimens. In the two best-preserved maxillaries (young individuals) from the Frenchman Formation, the "step" is present on SMNH P1927.824 but absent on the other (SMNH P2004.86). This variation is also shown in those large maxillaries from the Lance and Hell Creek formations collected by UALVP field parties: the "step" is present on UALVP 29729 (from BTB), but absent on UALVP 29727 (BTB) and 29738 (BCA). Furthermore, this "step" in the tooth row is also developed in extant *Crocodilurus* and *Tupinambis* (see Estes, 1964:fig. 48), and at least some of the fossil *Leptochamops* (see Estes, 1964:fig. 50). Therefore, the "area of reduced tooth

size" or the "step" is not unique for *Chamops segnis,* and, thus, cannot be regarded as a diagnostic character. It is difficult to evaluate this character without a complete survey of the dentition of teiids and related groups; however, it seems to us that the "step" is functionally significant, as it may correspond to the biting mechanism of the jaws; that is, it may be the area frequently used to hold prey (insects). Estes et al. (1988:162) regarded "a step in the maxillary tooth row to be a synapomorphy of Lacertiformes."

Second, the referral of several parietals to *Chamops segnis,* including UCMP 57147 (see Estes, 1964:fig. 49) is uncertain, because it is mainly "on the basis of size and frequency of occurrence" (Estes, 1964:104). There are other teiid species known from the same formation, and the specimens are disarticulated, being collected mostly by screen washing. Moreover, the size difference between *Chamops segnis* and other contemporaneous teiids is not great enough to separate the fragmentary skull elements one from another taxonomically. Therefore, it is difficult to recognize the natural association of the disarticulated parietals with the jaw material of *Chamops segnis,* unless other evidence, such as a more or less articulated specimen, is discovered. Furthermore, even if a complete skull of *Chamops* could be found and proved to have a parietal foramen, the presence of the foramen as a diagnostic character still is not warranted: ontogenetic evidence shows that loss of the foramen in most living species is a derived condition and must have been achieved quite recently in evolution (Presch, 1970). Therefore, the presence of a parietal foramen in teiids is a primitive condition, and, thus, is not a diagnostic feature for fossil species of teiids.

Synonyms of *Chamops segnis*. Estes (1964, 1983*a*) placed *Iguanavus teres* Marsh, 1892, *Lanceosaurus hatcheri* Gilmore, 1928, *Lanceosaurus compressus* Gilmore, 1928, and *Alethesaurus quadratus* Gilmore, 1928 in synonymy with *Chamops segnis*; we have compared the published data on these taxa (description, figures, and discussion), and offer the following comments:

Marsh (1892:451) founded *Iguanavus teres* on several unnumbered dorsal vertebrae (his "type specimens") from the Lance Formation, Wyoming. Gilmore (1928:17–18) designated and described the type specimen (YUM 530), and apparently confirmed the taxonomic status of the genus *Iguanavus.* Even later, Estes (1964, 1983*a*) synonymized *I. teres* with *Chamops segnis* on the basis of size and frequency of occurrence of the specimens, although no vertebrae of *Chamops* have ever been described. Marsh's naming of *Iguanavus teres* based on only vertebrae is unfortunate, because vertebrae in most cases provide little information for species identification. In other words, the nominal taxon *Iguanavus teres* is based on specimens that are inadequate, probably nondiagnostic at a lower taxon level; the type specimen (YUM 530) was never figured, and the species was never diagnosed. Thus, *Iguanavus teres* is a "nomen dubium" of ICZN (1985) or a "nomen vanum" of Simpson (1948) and Mones (1989); probably the type species *Iguanavus exilis* (see Marsh, 1872; Gilmore, 1928) is as well (Estes, 1983*a*). A "nomen dubium" or a "nomen vanum" is an invalid name that has no standing in zoology (ICZN, 1985; Mones, 1989), although each stands as a nominal species in nomenclature (see Simpson, 1948; Mones, 1989).

Gilmore's (1928) *Lanceosaurus* includes the type species *L. hatcheri,* and *L. compressus,* both later placed as synonyms of *Chamops segnis* by Estes (1964). The type specimen of *L. hatcheri* (USNM 10706) is a left dentary containing partly dissolved teeth. Estes (1964) stressed the eroded nature of the type and argued that a similar kind of erosion in some specimens of *Chamops* indicates they belong to the same species. However, to synonymize *Lanceosaurus* with *Chamops* is probably not valid, because USNM 10706 obviously differs from the dentary of *Chamops segnis* in having a more slender configuration, a much deeper subdental shelf, and a more restricted Meckelian canal. Therefore, USNM 10706 should not be referred to *Chamops segnis,* and is so poorly preserved that it shows no characters adequate to establish a species. In view of this fact, *Lanceosaurus hatcheri* should be regarded as a "nomen vanum". The other species, *L. compressus,* displays a similar condition, and should be treated the same as the type species.

Gilmore (1928) named *Alethesaurus quadratus* and placed it in the Teiidae. The holotype (USNM 10802) is a poorly preserved maxillary fragment "bearing four perfect teeth" as described, but there are actually only three and these are badly dissolved as photographed (see Gilmore, 1928:162, pl. 26, fig. 13). Estes (1964) reexamined the holotype and concluded that the specimen was a well-worn dentary fragment of *Chamops segnis,* which bears the "last few teeth." We agree with Gilmore's original identification of the specimen as a maxillary, as the dental shelf on the specimen is thin and plate-like, indicating a supradental rather than a subdental shelf; however, *Alethesaurus quadratus* is in fact founded

on a specimen that is inadequate for a generic or specific identification. Thus, in this study, we can neither revalidate the name, nor agree with placing it as a synonym of *Chamops segnis.* The posterior teeth of *Chamops* are widely tricuspid, and the shafts are strongly swollen or barrel-shaped; none of these features are shown on USNM 10802, although Gilmore (1928:162) mentioned "a vestigial denticle" at the base of the cutting edge of the teeth. In this paper, *Alethesaurus quadratus* is treated as a "nomen vanum," since it is "based on types which are inadequate for definitive diagnosis" (Mones, 1989:233).

Problematic Reports and Misidentified Specimens. C. M. Sternberg (1951) identified a jaw fragment (NMC 8891) as "*Chamops* cf. [*C.*] *segnis*" (incorrect syntax in using "cf."; for comments see Lucas, 1986; Estes, 1987). The specimen was collected from the Upper Cretaceous Wapiti Formation, which is partially correlative with the Horseshoe Canyon Formation of central Alberta (Tanke, 1988; Dodson and Currie, 1990), in the Kleskun Hills, northwestern Alberta. Although the specimen was unavailable for this study, the original description and the illustration (C. M. Sternberg, 1951:256) show that NMC 8891 differs from *Chamops segnis* in having relatively high-crowned and much less swollen teeth, as well as having a subdental shelf that sharply decreases in depth posteriorly. Therefore, the specimen NMC 8891 is probably not a jaw of *Chamops segnis,* and a restudy of the specimen is needed.

Waldman (1970) described a lower jaw ramus (NMC 13563) from the Oldman Formation as "*Chamops* sp." Estes (1983*a*) subsequently referred the specimen to *Chamops segnis,* and restored the mandible of *C. segnis* based on this specimen (Estes, 1983*a*:fig. 22; but see discussion on *Sphenosiagon* below). But a recent restudy of this specimen resulted in its removal from *Chamops,* and referral to *Sphenosiagon* (Gao and Fox, 1991). The specimen NMC 13563 shows a lightly built and wedge-shaped dentary, narrow subdental shelf, and poorly defined sulcus dentalis. All of these are diagnostic features for *Sphenosiagon,* differing from those of *Chamops* and other teiids. The teeth of NMC 13563 are partly dissolved, showing no cusp pattern, but another specimen (UALVP 29742) clearly shows that the crowns of this lizard are unicuspid, rather than tricuspid as in *Chamops* (see later discussion on *Sphenosiagon*).

Sahni (1972) referred three specimens (AMNH 8486–8488) from the Judith River Formation, Montana, to *Chamops segnis,* thereby extending the geologic record of this particular species from Lancian to Judithian. However, these specimens (see Sahni, 1972:fig. 8A–D) are too poorly preserved to justify a definite referral at species level to *Chamops segnis,* although they are probably referrable to *Chamops* at the generic level. AMNH 8486 (Sahni, 1972: fig. 8A, B) is a robust dentary having only tooth bases preserved. The specimen shows no indication of having short-crowned, broadly tricuspid, and weakly heterodont teeth, which are characteristic of the Lancian *Chamops segnis.* Another specimen, AMNH 8488 (Sahni, 1972:fig. 8C, D), is a maxillary fragment with four anterior teeth. Once again, the specimen shows none of the diagnostic characters for *Chamops segnis,* although short and robust anterior teeth, and robustness of the maxillary may count as indication of *Chamops* affinity broadly. Through personal observation of these specimens, it seems to us that they can be more appropriately referred as to "Teiidae, gen. et sp. indet.". If the boat-shaped dentary configuration of AMNH 8486 can be regarded broadly as a significant similarity to *Chamops,* the specimen can be identified in no further detail than "*Chamops* sp."

Armstrong-Ziegler (1980) reported the occurrence of *Chamops segnis* in the Fruitland Formation, New Mexico. The specimen on which this report is based is a dentary fragment having one tooth and the base of another (MNA Pl. 1613). It shows a subpleurodont dentition that is indicative of the family Teiidae, but shows no diagnostic features at either generic or specific levels. The specimen is too fragmentary to be identifiable as *Chamops segnis* or even *Chamops,* and may be more appropriately referred to as "Teiidae, gen. et sp. indet."

Sullivan (1981) identified another specimen (UNM FKK-038a) from the Fruitland Formation as "cf. *Chamops segnis,*" and stated that "this specimen, although somewhat larger than previously described specimens (Estes, 1964), agrees in every respect with the species *Chamops segnis,* where heterodonty is little pronounced and tooth crowns are not swollen" (Sullivan, 1981:77). The specimen was originally described as "posteriad teeth are tricuspid; anteriad teeth are pointed and slightly recurved" (Sullivan, 1981:77). Probably based on this description, Estes (1983*a*) referred this specimen to *Chamops segnis.* However, the above-mentioned statement and description are not in agreement with the illustrations of the specimen (see Sullivan, 1981: text fig. 4.1). The drawings show that the anterior teeth on the specimen are either partially dissolved

or broken, and the posterior teeth show no indication of having tricuspid or barrel-shaped crowns. From the illustrations, no evidence is available to show affinities with *Champops segnis,* but the extremely heavy deposit of cementum around the tooth bases and the large replacement pits show resemblance to some Tertiary tupinambines (e.g., *Tupinambis huilensis*; see Estes, 1983*a*:fig. 23). Therefore, although there is not much doubt that UNM FKK-038a represents a teiid, its referral to *Champops segnis* is questionable. When more specimens from the same formation become available, this specimen should be restudied.

Champops sp.
(Fig. 7F–J)

Referred Specimens.—UALVP 29816–29818, 29820, 29826 (total: five), fragmentary maxillaries; UALVP 29819, fragmentary dentary.

Locality and Horizon.—MR-6 and MR-20 localities, Verdigris Coulee, approximately 30 km east of the village of Milk River, southern Alberta; upper member of the Milk River Formation (Aquilan), Upper Cretaceous.

Description.—The specimens UALVP 29816 and 29826 (Fig. 7F, G) are both the posterior part of left maxillaries, each having five teeth preserved. The maxillary teeth are short, stout, and tricuspid. Although swollen in lateral view, the tooth bases are slightly compressed anteroposteriorly. These teeth are evidently subpleurodont, being attached to a low lateral parapet for about one-third of the tooth height. Dorsal and medial to the tooth row is a well-developed supradental shelf on UALVP 29826 (broken on 29816), which carries a shallow but well-defined sulcus dentalis medial to the tooth bases.

The third fragmentary maxillary (UALVP 29817, Fig. 7H) has the posteriormost five teeth and the broken base of another preserved. The specimen shows the same tooth form as that of the two maxillaries described above, but has replacement pits developed at the bases of the last and the fourth posteriormost teeth. The posterior interior alveolar foramen, as in the Lancian species *Champops segnis,* opens above the fifth tooth position from the back.

Another maxillary, UALVP 29818, shows a short external premaxillary process and the more or less plate-like base for the medial process. A notch between the two processes is clearly recognizable on the specimen. The nasal process of the bone rises abruptly behind the notch for the naris, forming a steep lateral wall of the maxillary. Although broken dorsally and posteriorly, the preserved part shows that the dorsal process of this species is higher and more steep anteriorly than that of the Lancian *Champops segnis* (see Estes, 1964:fig. 47). The maxillary fragment shows the anteriormost six tooth positions (four teeth and the broken base of two others). The teeth are conical but have swollen bases, and the tips of the crowns are slightly recurved.

The tooth form of this species is better shown on UALVP 29819 and 29820 (Fig. 7I, J). The former is a fragmentary right dentary having three teeth and the latter a left maxillary fragment bearing four teeth. The teeth are short and subpleurodont, and the tooth shafts are swollen, having a heavy deposit of cementum at the tooth bases. Having a "bottle neck" constriction, the crowns are slightly narrower than the swollen shafts, and the middle and posterior parts of the tooth row are broadly tricuspid. The main cusp is much stronger than the side cusps, and the anterior side cusp is, in most cases, more prominent than the posterior one. The unworn teeth on UALVP 29819 show that the crown surface has faint wrinkling or striations, which are shown more clearly lingually than labially.

Discussion.—The six specimens described above represent the geologically oldest records of the genus *Champops,* as the specimens were collected from the upper member of the Milk River Formation, which is Aquilan in age (see the section "Geological Setting" above). The teeth of these specimens resemble those of *Champops segnis* (from all Lancian sites) more closely than those of any other early teiids in already showing a tendency towards the apomorphic swollen crowns which characterize that species, and the more posterior teeth are strongly tricuspid, as in *C. segnis,* although the side cusps are smaller relative to the central cusp than in the Lancian form. In addition, the vertically directed anterior edge and the height of the nasal process (shown in UALVP 29818) differ from those of *Champops segnis* (see Estes, 1964:fig. 47). Importantly in the Milk River specimens, the crowns are taller and less swollen than in *C. segnis* specimens of comparable size, as if representing membership in a transformation series between ancestral states in which the tooth shafts are columnar and straight-sided (see, e.g., Winkler et al., 1990, for Early Cretaceous teiids) and the barrel-like shafts of *C. segnis.* In the light of these comparisons, we accept as a working hypothesis that the Milk River specimens represent a species of *Champops* more primitive than *C. segnis,* with the morphological differences corroborated by the 18 Myr chronological gap that separates Milk River from Lancian horizons; in the absence of more extensively preserved material, this species is best designated "*Champops* sp."

Genus *Socognathus* Gao and Fox, 1991

Type Species.—*Socognathus unicuspis* Gao and Fox, 1991.

Range.—Upper Cretaceous, North America.

Diagnosis.—As for the type and only known species.

Socognathus unicuspis Gao and Fox, 1991
(Fig. 8, 9)

Holotype.—UALVP 29739, an incomplete left dentary having 11 well-preserved teeth and the bases of six others.

Type Locality and Horizon.—Railway Grade locality, in Sec. 29, Tp. 21, R 12, W 4, southeastern Alberta; Upper Cretaceous Oldman Formation (Judithian).

Referred Specimens.—UALVP 29910–29911, incomplete tooth-bearing maxillaries; UALVP 29732, 29736, 29740, 29743–29745, and RTMP 82.24.57, incomplete tooth-bearing dentaries; all the referred specimens were collected from the Irvine locality (legal description below).

Known Distribution.—Upper Cretaceous Oldman Formation (Judithian), southeastern Alberta. Possible occurrence of the genus in the Hell Creek Formation is indicated by an unnumbered jaw fragment in the UALVP collections from the BCA locality, but identity cannot be confirmed owing to the poor preservation of the specimen.

Diagnosis (Revised from Gao and Fox, 1991).—Relatively large Late Cretaceous teiid differing from other teiids in having a unique combination of the following character states: dentary greatly elongate and robust; mandibular symphysis strongly enhanced by ventral bony buttress; marginal teeth not crowded along tooth row, but variable in spacing and orientation; teeth tall, with straight anterior and posterior sides, somewhat compressed anteroposteriorly and recurved, set at an oblique angle to long axis of jaw; tooth crowns unicuspid, with cusp pointed, inclined somewhat posterolingually, and having moderately strong anterior ridge and weaker posterior ridge curving lingually from apical cusp; tooth attachment subpleurodont, with lateral parapet low, about one-third of tooth height.

Description.—The holotype (Fig. 8, 9A, B) is a left dentary having 11 complete teeth and the bases of six others, with probably the posteriormost one or two teeth missing on account of breakage. The dentary is elongated but robust, and is relatively straight when viewed from above. Medially, the dentary bears a sturdy subdental shelf, the dorsal (subdental) ridge of which borders a well-developed sulcus dentalis along the medial side of the tooth row. The shelf gently narrows posteriorly, but anteriorly turns slightly dorsomedially to the mandibular symphysis. The ventral side of the shelf bears a narrow but clearly defined groove for the dorsal spleniodentary articulation, which terminates anteriorly below the sixth tooth position, and extends posteriorly to the end of the dental shelf. Anteriorly, the dentary has a strong ventral bony buttress, which would greatly strengthen the mandibular symphysis of this teiid in life. Posteriorly, the inferior alveolar canal opens into the Meckelian canal through the posterior interior alveolar foramen below the 13th tooth position. The widely open Meckelian canal on the specimen indicates a significant hypertrophy of the splenial.

The dentary teeth are basically unicuspid, with no tendency towards developing tricuspid crowns as is characteristic of *Chamops*, although the posterior teeth have stronger anterior and weaker posterior ridges curving ventrolingually; faint striations are present lingually on the apical cusp in some specimens. The

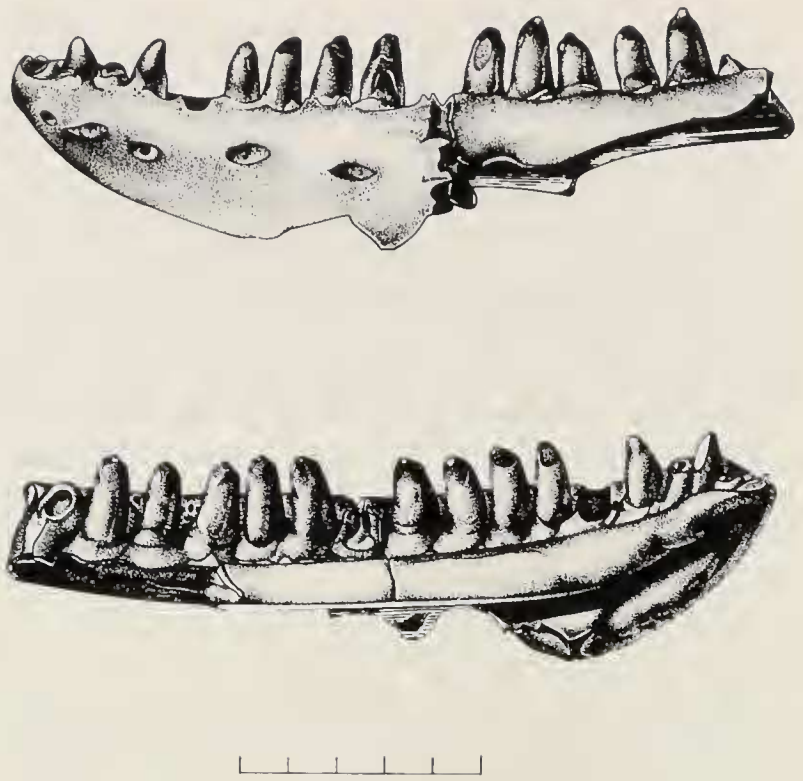

Fig. 8.—*Socognathus unicuspis*, Oldman Formation, Alberta: UALVP 29739 (holotype), incomplete left dentary, lateral (above) and medial (below) views. Scale = 5 mm.

crowns are generally bent lingually but variably so; the teeth also vary in size and spacing posteriorly along the tooth row (best shown on UALVP 29736, Fig. 9C), in contrast to the more regular spacing, size, and orientation of the teeth in *Chamops*. The tooth bases are slightly expanded laterally; a deposit of cement is clearly shown around the bases. The lateral parapet of the jaw is low, about one-third of the tooth height; thus, the dentary teeth are subpleurodont in mode of attachment. The holotype (from a large, evidently mature, individual) shows a suppression of tooth replacement, but resorption pits can be seen on smaller specimens (e.g., UALVP 29740). The tooth row of the holotype is straight, but variation of this character is seen in UALVP 29736, which shows a strong curvature as in *Leptochamops*. The number of teeth anterior to the posterior interior alveolar foramen is about 13, posterior to the foramen five or six; therefore, the complete tooth row is estimated to include 18–20 teeth. The posterior teeth are enlarged, resulting in a weakly developed heterodonty along the tooth row.

The external surface of the dentary is strongly convex dorsoventrally, and strongly swollen laterally as a consequence of the posterior expansion of the Meckelian canal. On the holotype, the inferior alveolar foramina on this surface increase posteriorly in size, and the spaces between the foramina lengthen as well, but these attributes seem to be somewhat irregular on other specimens, such as UALVP 29736. The lower and posterior part of the holotype, as in most other specimens, is missing as a consequence of breakage; however, the well-preserved anterior part suggests that the lower jaw is deeper than that of *Leptochamops*, but significantly shallower than that of the contemporaneous teiid *Glyptogenys* Gao and Fox, 1991. Except as noted above, these characters do not change across the range in size of the dentaries in the present collection, and the larger specimens no more resemble dentaries of other species described here than do the smaller ones. Denton and O'Neill (1995) cited significant ontogenetic changes in coronal morphology in *Prototeius*, their new teiid from the Campanian of New Jersey. Comparable changes

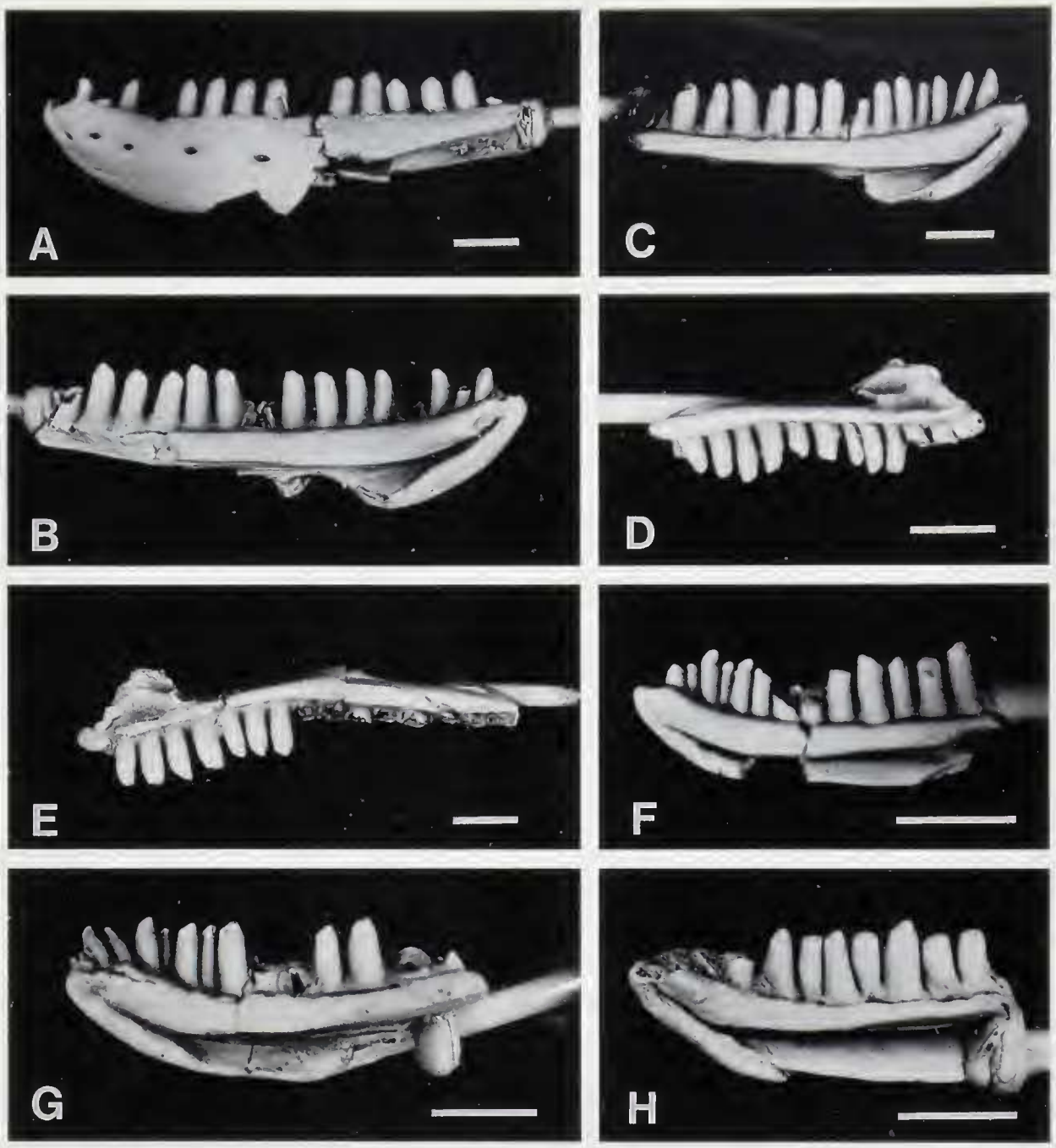

Fig. 9.—*Socognathus unicuspis,* Oldman Formation, Alberta: A, B, UALVP 29739 (holotype), incomplete left dentary, lateral and medial views; C, UALVP 29736, left dentary, medial view; D, UALVP 29910, left maxillary, medial view; E, UALVP 29911, right maxillary, medial view; F, UALVP 29743, right dentary, medial view. G, UALVP 29744, right dentary, medial view; H, RTMP 82.24.57, right dentary, medial view. Scale = 2 mm.

are not present in the dentaries referred to *Socognathus unicuspis,* even though the smallest (UALVP 29743) is less than half the size of the largest (UALVP 29739, holotype).

UALVP 29910 (Fig. 9D) is an incomplete left maxillary bearing nine teeth and the bases of three others. The specimen is smaller than the holotype dentary, indicating that it is from a younger individual. The maxillary is broken above the superior alveolar foramina and behind the 12th tooth position, but the anterior end is nearly complete. Medially, the specimen bears a strong supradental shelf and a well-developed sulcus dentalis. The posterior interior alveolar foramen is located above the 12th position in the maxillary tooth row (the posteriormost tooth remaining in the specimen). The first three teeth are broken off, with only the bases preserved, but the remaining teeth are complete, except for the two in the middle of the tooth row, which have the apex of the crown broken off. As in the dentary specimens, the maxillary teeth are unicuspid, subpleurodont, and variable in size, spacing, and curvature along the tooth row. In lateral view, UALVP 29910 has a very short premaxillary process. The superior alveolar foramina positioned laterally above the tooth row are small and are more or less equally spaced from one another, but the facial process above the foramina is not preserved.

The other specimen in the collection (UALVP 29911, Fig. 9E) is a right maxillary fragment with seven teeth and the broken bases of nine others. The specimen is larger and more robust than UALVP 29910, and shows a nearly complete tooth count of the maxillary tooth row. The first tooth is broken, followed by seven complete teeth, and tooth bases of nine others. The posteriorly narrowed dental groove indicates that the tooth row is nearly complete, with probably one, at most two, positions missing; therefore, the maxillary probably had about 18 tooth positions. The well-preserved teeth on this specimen show the same crown pattern and tooth attachment as the holotype dentary,

but have a "step" of the tooth row at the fifth through the eighth positions, where the teeth are significantly smaller than those anterior to them (also in UALVP 29910). This kind of "step" is also seen in *Chamops* and other lizards (see above discussion on *Chamops*). Unlike UALVP 29910, the ventral view of this specimen shows that the maxillary tooth row is strongly curved, corresponding to the facial constriction in front of the orbits, and it is strongly flexed dorsally as well, in contrast to the maxillary of *Chamops segnis* (e.g., UALVP 29729), in which these surfaces are relatively straight. As in UALVP 29910, the posterior interior alveolar foramen is open above the supradental shelf at the level of the 12th tooth position. Posterior to the foramen, the supradental shelf bears a well-developed groove along the lateral border of the maxillary. This groove is a clear indication of a tongue-and-groove articulation of the maxillary with the anterior ventral process of the jugal, which is unknown.

The internal surfaces of the maxillary of *Socognathus* differ significantly from those of *Chamops* and *Leptochamops,* which are virtually identical in these regards. For example, the posterior interior alveolar foramen opens more anteriorly in *Socognathus* and the articulation surface for the palatine is significantly deeper and anteriorly more extensive—anatomical differences that supplement those of the dentition in distinguishing *Socognathus* from *Chamops* and *Leptochamops.*

Discussion.—The referral of *Socognathus* to the Teiidae is basded mainly on two character states: hypertrophy of the splenial (as indicated by the widely open Meckelian canal), and a heavy basal deposit of cementum; both are recognized synapomorphies of the family Teiidae (MacLean, 1974; Presch, 1974*b*; Estes, 1983*a*; Estes et al., 1988). Some other character states, such as strong subdental shelf and well-developed sulcus dentalis, are also indicative of the Teiidae.

Socognathus unicuspis is now known from several well-preserved, tooth-bearing dentaries and maxillaries, as enumerated above. In addition, several uncatalogued fragmentary specimens from both the Railway Grade and Irvine localities are also referrable to this species. A comparison of the holotype dentary with the referred specimens allows reconstruction of the dentary proportions of this teiid, and shows that *Socognathus* differs in both tooth form and structure of the dentary from other teiids of the same age, including *Glyptogenys, Sphenosiagon,* and *Gerontoseps* Gao and Fox, 1991, known from the same formation. A strong mandibular symphysis enhanced by a ventral bony buttress seems to be unique for *Socognathus unicuspis,* and hence offers no information about its relationship to other teiids. However, the large size of this lizard, variable spacing of the marginal teeth, and the tendency of the teeth to increase in size posteriorly (resulting in a certain degree of heterodonty) are unique resemblances to extant *Tupinambis,* a large omnivorous teiid distributed in tropical South America. Therefore, this Judithian teiid is probably referrable to the subfamily Tupinambinae (sensu Presch, 1983), which includes the extant genera *Tupinambis, Callopistes, Crocodilurus, Dracaena,* and the Late Cretaceous fossil genus *Chamops* (Estes, 1964, 1983*a*; Presch, 1983). Many large specimens of *Socognathus* show no resorption pits, indicating suppression of tooth replacement in adults, which has also been recognized in *Tupinambis* (MacLean, 1974).

UALVP 29743–29744 (Fig. 9F, G) and RTMP 82.24.57 (Fig. 9H) from the Irvine locality are three small dentaries referred to *Socognathus unicuspis* with some uncertainty. The three specimens show a similar tooth form (cusp pattern) to the holotype, but the dentaries are slightly more slender, and the anterior teeth are packed closely together. Furthermore, RTMP 82.24.57 shows that the subdental shelf sharply decreases in thickness posteriorly, differing from other specimens mentioned above. These three dentaries are tentatively referred to *Socognathus unicuspis,* awaiting further study of more and better preserved specimens to clarify their taxonomic position.

Genus *Sphenosiagon* Gao and Fox, 1991

Type Species.—*Sphenosiagon simplex* Gao and Fox, 1991.

Range.—Upper Cretaceous, North America.

Diagnosis.—As for the type and only known species.

Sphenosiagon simplex Gao and Fox, 1991 (Fig. 10, 11A–D)

Chamops sp. Waldman, 1970:546, fig. 2–3.

Holotype.—UALVP 29742, incomplete left mandible having the splenial firmly articulated with the dentary, and having eight posterior teeth and the base of another.

Type Locality and Horizon.—Outcrop of the Oldman Formation near Irvine, in Sec. 31, Tp. 11, R 2, W 4, about 40 km east of Medicine Hat, southeastern Alberta; Upper Cretaceous Oldman Formation (Judithian).

Referred Specimens.—NMC 13563, a tooth-bearing right mandibular ramus collected by C. M. Sternberg from a locality near Steveville, Alberta (Waldman, 1970). UALVP 29836–29837, fragmentary tooth-bearing dentaries from MR-6 locality of the Milk River Formation.

Known Distribution.—Upper Cretaceous Oldman Formation (Judithian), and the upper member of the Milk River Formation (Aquilan), southern Alberta.

Diagnosis (Revised from Gao and Fox, 1991).—

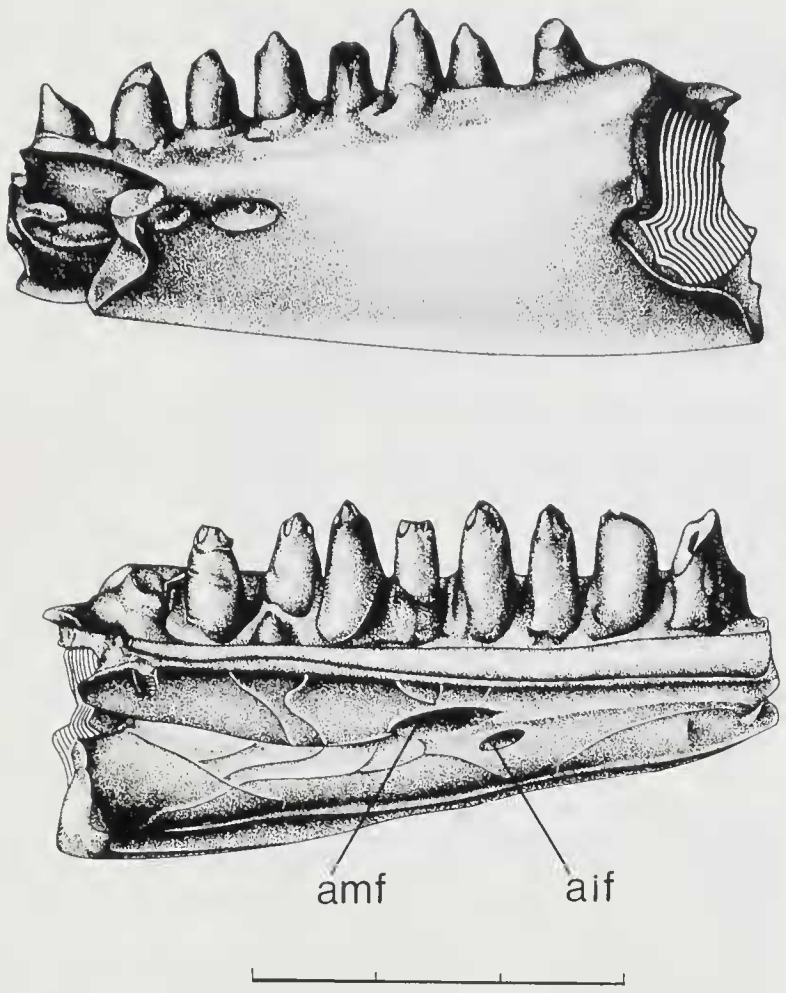

Fig. 10.—*Sphenosiagon simplex*, Oldman Formation, Alberta: UALVP 29742 (holotype), incomplete left mandible, lateral (above) and medial (below) views. Scale = 3 mm. Abbreviations as in Fig. 2.

A Late Cretaceous teiid differing from other teiids in having in combination the following character states: dentary shallow, strongly bilaterally compressed and wedge-shaped, with straight dorsal and ventral margins along tooth-bearing parts; subdental shelf narrow; sulcus dentalis poorly defined; dentary teeth relatively short and regularly arranged; tooth shafts straight, pillar-like, little expanded transversely even at base, not set obliquely across jaw; tooth crowns unicuspid, but not recurved, lacking lingual striae, with anterior apical crest stronger than posterior crest; tooth attachment tending to be subacrodont, with lateral parapet one-third or less of tooth height.

Description.—The holotype UALVP 29742 (Fig. 10, 11A, B) is an incomplete tooth-bearing left dentary with a firmly articulated splenial. The mandibular symphysis and the postdentary part of the jaw are missing. Sharply tapering anteriorly, the specimen clearly shows that the lower jaw was wedge-shaped, lacking the boat-shaped curvature along the ventral border that is seen in some other teiids (e.g., *Chamops, Socognathus*). As shown as well on the referred specimens, the mandible is laterally compressed so that its lateral surface is almost flat and not expanded posteriorly, differing from *Socognathus* and other contemporaneous teiids that have a much more convex lateral surface of the dentary. The small inferior alveolar foramina are unevenly spaced, and the posteriormost foramen is located anterior to the midpoint of the tooth row. The same arrangment of these foramina is also shown on NMC 13563, a right mandibular ramus that preserves a more nearly complete configuration of the jaw.

The medial surface of the jaw is concave, and is occupied largely by the hypertrophied and wedge-shaped splenial. Two Meckelian foramina (anterior inferior alveolar foramen and anterior mylohyoid foramen) are close to each other and penetrate the splenial to open into the Meckelian canal close to the midpoint of the tooth row. The splenial is firmly attached, but not fused, to the dentary, having clearly recognizable dorsal and ventral spleniodentary sutures. The ventral suture is developed along the ventral edge of the jaw, not crossing laterally beyond the ventral midline. The slender subdental shelf is distinctive: the anterior maximum depth of the shelf is no more than half of the tooth height, and is greatly diminished posteriorly. The dorsal ridge of the shelf is so poorly developed and so close to the tooth row that a sulcus dentalis is barely recognizable, in contrast to the well-developed sulcus in *Chamops* and *Socognathus*.

The holotype has eight posterior teeth and the base of another preserved. A comparison with NMC 13563 (referred specimen with a complete posterior end of the tooth row) suggests that the holotype may have the posteriormost one or two teeth missing (both specimens have the anterior end broken off). Among the preserved teeth, three are complete, and the remaining ones have the crowns partly broken. The crowns are unicuspid with a pointed cusp forming an apex and a faint ridge on both the mesial and distal sides of the cusp. The tooth shafts are straight and are thickened toward the tooth bases, giving a pillar-like configuration. An extensive, heavy basal deposit of cementum is clearly visible on the holotype and referred specimens. The dentary teeth are moderately spaced, forming a relatively straight tooth row. The attachment of these teeth can be called subpleurodont, but the lateral parapet is so low (no more than one-third of the tooth height) and the dental gutter is so poorly defined, that the term subacrodont is probably more appropriate. One of the tooth positions on the holotype shows a new tooth erupting posteromedial to the base of the tooth to be replaced (see Fig. 10). The replaced tooth, still in the functional tooth row, has been slightly pushed away laterally from the midline of the tooth row, showing a kind of irregular replacement compared to the "standard" teiid pattern, in which the replacement teeth are developed posteromedially, in subcircular resorption pits (Romer, 1956).

In the UALVP collections, two specimens from the upper member of the Milk River Formation document the Aquilan occurrence of *Sphenosiagon simplex*. One of the two (UALVP 29836, Fig. 11C) is the posterior part of a right dentary, with five complete teeth and the broken base of another. The dentary is larger than the holotype, but clearly resembles the latter in tooth form, spacing, and the mode of tooth attachment. The splenial is missing, leaving the Meckelian canal widely open, showing that a large posterior interior alveolar foramen opens under approximately the fourth posteriormost tooth position; the dorsal and ventral borders of the dentary that define the Meckelian canal are straight, and in the context of the overall shape of the fragment, indicate that the dentary was shallow and wedge-shaped, as in *Sphenosiagon*. The other specimen (UALVP 29837, Fig. 11D) is the dentary fragment of an old individual, as evidenced from its size and robustness, and evident suppression of tooth replacement. Although fragmentary, this specimen is clearly referrable to *Sphenosiagon simplex* based on its char-

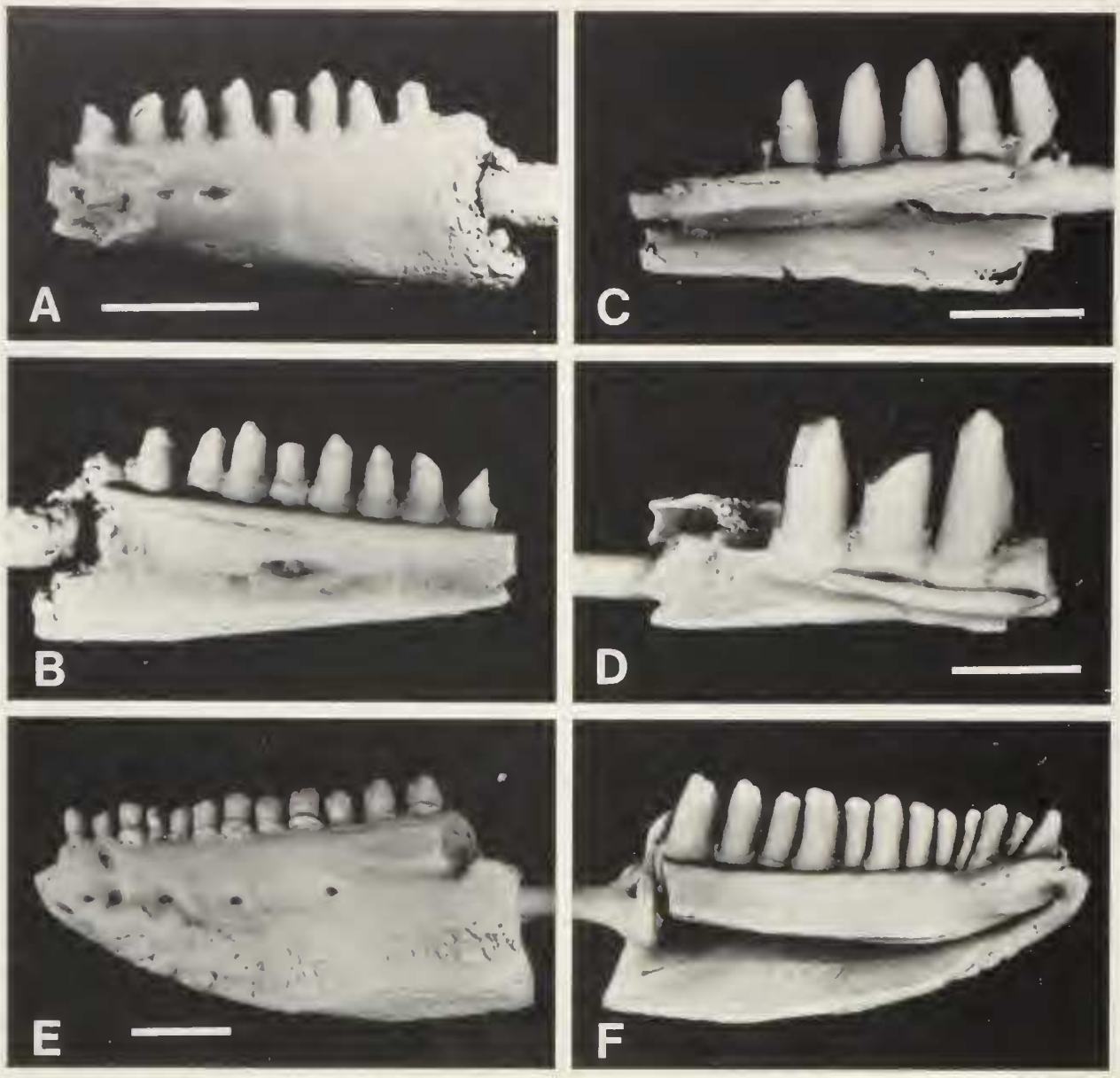

Fig. 11.—*Sphenosiagon simplex,* Oldman Formation, Alberta: A, B, UALVP 29742, holotype, incomplete left mandible, lateral and medial views; Milk River Formation, Alberta: C, UALVP 29836, right dentary fragment, medial view; D, UALVP 29837, left dentary fragment, medial view. *Glyptogenys ornata,* Oldman Formation, Alberta: E, F, UALVP 29735 (holotype), left dentary, lateral and medial views. Scale = 2 mm.

acteristic crown pattern and a distinct groove below the subdental shelf for the spleniodentary articulation.

Discussion.—As described above, *Sphenosiagon simplex* from the Oldman and Milk River formations has a large splenial covering almost the entire medial side of the dentary and a heavy deposit of cementum around the tooth bases; therefore, the lizard is referrable to the family Teiidae.

Taxonomic Assignment of NMC 13563. Waldman (1970) described a right mandible (NMC 13563) from the Oldman Formation, southeastern Alberta, which he identified as *Chamops* sp.; this specimen was subsequently referred to *Chamops segnis* by Estes (1983*a*:95). A reconstruction of the mandible of *Chamops segnis* given by Estes (1983*a*:fig. 22) is also based on NMC 13563. However, restudy of this specimen strongly indicates that NMC 13563 does not belong to *Chamops segnis* and should be allocated to *Sphenosiagon simplex,* as Gao and Fox (1991) demonstrated.

First, a comparison of NMC 13563 with the holotype of *Sphenosiagon simplex* indicates that the two specimens belong to the same species: they show the same unique shape of the jaw, the same development of the splenial that is firmly attached to the dentary, a much more narrow subdental shelf than in *Chamops segnis,* a poorly defined sulcus dentalis, and the same kind of tooth attachment. Second, although the tooth crowns on NMC 13563 have been partially dissolved diagenetically (only at the tips, not more ventrally), those on the holotype (UALVP 29742) are unambiguously unicuspid, not tricuspid as in *Chamops segnis,* nor do the tooth shafts display the barrel-like proportions that were illustrated in Estes' (1983*a*:fig. 22) figure for NMC 13563; in fact, Estes' figure differs substantially

from that of Waldman (1970:fig. 2), which is the more accurate. For example, no "surangular window" is preserved on NMC 13563 (see Estes, 1983*a*:94), and the so-called "coronoid," which both Waldman (1970) and Estes (1983*a*) have shown, is actually a piece of unidentifiable postdentary bone glued into the position of a coronoid. Therefore, future study of better preserved specimens may well change the reconstruction of the jaw.

Waldman (1970) estimated that the full tooth count of NMC 13563 is about 15, which is correct. His claim, however, that the "dental gutters are present on both sides of the tooth-row" (Waldman, 1970:546) is incorrect and unlikely for any lizard taxon. In fact, in NMC 13563, only the eighth tooth from the back is located more medially than the others, leaving a short space from the low lateral parapet of the dentary. This tooth is not fully functional, but is still developing and is not yet attached to the lateral parapet of the jaw. All of the remaining teeth are attached to the low lateral parapet, and there is no dental gutter along the labial side of the tooth row.

Comments on Several Characters of *Sphenosiagon simplex*. The Judithian teiid *Sphenosiagon simplex* clearly shows several osteological characters that are worth special notice. One of these characters is the tendency towards subacrodonty. The dental gutter in this species is so poorly developed, and the lateral parapet of the jaw is so low, that the term subacrodont is almost appropriate. The tooth attachment in teiids can be either subpleurodont, as in extant *Kentropyx* Spix, 1825 and fossil *Leptochamops*; or subacrodont, as in extant *Teius* Merrem, 1820 and fossil *Haptosphenus* (Estes, 1964; see also later description). There is no true acrodont condition known in the Teiidae; however, a subacrodont pattern has independently evolved in all three subgroups of the family (Polyglyphanodontinae, Teiinae, and Tupinambinae; sensu Presch, 1983) as a more derived condition than subpleurodont. The subacrodonty is known from fossil polyglyphanodontines, such as the Campanian *Adamisaurus* Sulimski, 1972, and the Maastrichtian *Haptosphenus* and *Polyglyphanodon* Gilmore, 1940 (probably including *Paraglyphanodon* Gilmore, 1940); and from fossil and extant teiinines, such as *Peneteius* Estes, 1969*a*, and *Dicrodon* Duméril and Bibron, 1839. It is also known from extant tupinambinines, such as *Dracaena* Daudin, 1802. As far as is known among Late Cretaceous teiids, *Adamisaurus* and *Haptosphenus* demonstrate the most derived condition of subacrodonty in the family Teiidae.

Another character worth noting is the articulation of the splenial with the dentary. Unlike most fossil teiids, in which the splenial is often lost before burial, two specimens (holotype and NMC 13563) of *Sphenosiagon* have the splenial firmly attached to the dentary, even though the lower jaw is lightly built. A strong interlocking articulation between the splenial and the dentary may play a key role in the retention of the splenial. Two more fragmentary specimens (UALVP 29736, 29837) show that a deep groove is developed posteriorly on the ventral side of the subdental shelf. This groove differs from that of other teiids in having a ventromedial tongue-like structure that prevents the splenial from sliding ventrally. It could be that this type of articulation has prevented the loss of the splenial in *Sphenosiagon simplex*. The functional meaning of this structure is unclear, but might be related to the feeding habits of this lizard, coupled with the nearly subacrodont dentition.

It is possible that preservation of the relatively fragile dentary with the splenial in articulation reflects a taphonomic factor: the Irvine locality, where the holotype of *Sphenosiagon simplex* was obtained, may represent an "in-channel locality" (Brinkman, 1990), one containing a locally derived concentration of microfossils (Eberth, 1990*b*). However, Waldman (1970:542) thought that NMC 13563 had formed "part of the faeces of a crocodile of the genus *Leidyosuchus,*" as he stated that the specimen was found "between the first sacral rib and the anterior margin of the left ischium, [and] together with the curiously eroded teeth, is, to me, highly suggestive of digested material" (Waldman, 1970:546). This interpretation seems to be supported by recent experiments on crocodilian digestion, which show that teeth defecated by crocodiles lack enamel, but are often complete in other respects (Fisher, 1981). If NMC 13563 is indeed coprolitic in origin, the holotype (UALVP 29742) certainly represents another type of preservation under quite different conditions, because no "digestive demineralization" is shown on the specimen. The two specimens from the Milk River Formation are fragmentary and do not retain the splenial. This type of preservation may reflect the fact that the MR-6 locality represents a paleofacies that is slightly different from the Irvine locality.

Genus *Glyptogenys* Gao and Fox, 1991

Type Species.—Glyptogenys ornata Gao and Fox, 1991.

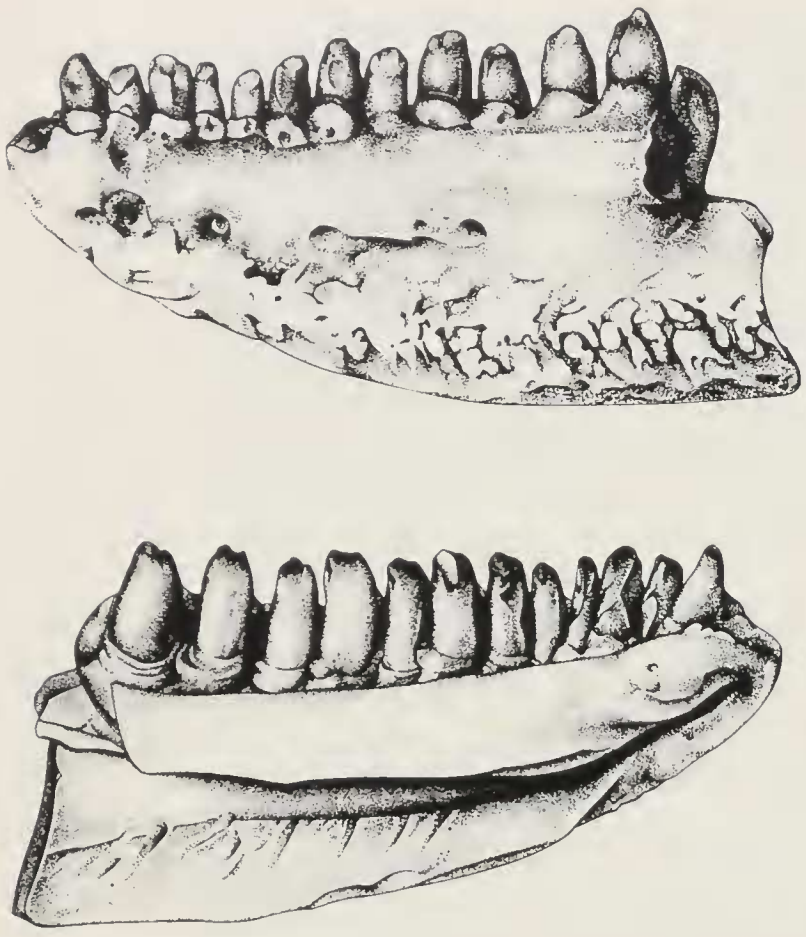

Fig. 12.—*Glyptogenys ornata,* Oldman Formation, Alberta: UALVP 29735 (holotype), incomplete left dentary, lateral (above) and medial (below) views. Scale = 5 mm.

Range.—Upper Cretaceous, North America.

Diagnosis.—As for the type and only known species.

Glyptogenys ornata Gao and Fox, 1991
(Fig. 11E, F, 12)

Holotype.—UALVP 29735, incomplete left dentary bearing 12 well-preserved teeth and bases for two others.

Type Locality and Horizon.—Outcrop of the Oldman Formation near Irvine, in Sec. 31, Tp. 11, R 2, W 4, about 40 km east of Medicine Hat, southeastern Alberta; Upper Cretaceous Oldman Formation (Judithian).

Referred Speciemens.—UALVP 2036, 29756, 29758–29759, 29913, 29767, 29769, all tooth-bearing dentaries, and all topotypic but UALVP 29758, from the Railway Grade locality of the same formation.

Known Distribution.—Upper Cretaceous Oldman Formation (Judithian), southeastern Alberta. Several unnumbered dentary fragments indicate possible occurrence of this lizard in the Milk River Formation (Aquilan), but this needs support from better preserved specimens.

Diagnosis (Revised from Gao and Fox, 1991).—A relatively large Late Cretaceous teiid that differs from other fossil and extant teiids in having the following combination of character states: dentary deep, massively built, and, in at least adult individuals, heavily ornamented below inferior alveolar foramina; subdental shelf significantly deeper than in other primitive teiids, maximum depth of which almost equals height of anterior dentary teeth; sulcus dentalis deep, but narrow, with medial wall appressed close to tooth bases; mandibular symphysis weak, lacking robust ventral buttress; dentary teeth heterodont, closely spaced, anteroposteriorly compressed, standing parallel to each other to form comb-like structure, and set obliquely to long axis of jaw; crowns slightly recurved, unicuspid anteriorly, bicuspid posteriorly, with main cusp in posterior position and anterior cusp smaller but prominent; tooth bases strongly widened transversely, having thick, ring-like deposit of cementum; tooth attachment subpleurodont, with lateral parapet about half of tooth height.

Description.—The holotype UALVP 29735 (Fig. 11E, F, 12) is an incomplete but well-preserved left dentary, broken immediately behind the 14th tooth position. The dentary is deep, massively built, laterally compressed, and probably proportionally shorter than that of *Socognathus.* It has a deep boat-shaped curvature along the ventral border, but tapers anteriorly and terminates with an extremely weak symphysis in relation to the size and robustness of the jaw. The symphysis lacks a ventral bony buttress, and is sharply different in this aspect from the jaw of *Socognathus,* besides having other differences in general proportions of the jaw and tooth form.

Medially, the dentary bears a deep and strong subdental shelf, the maximum depth of which is almost equal to the height of the anterior dentary teeth. The subdental ridge of the shelf forms the medial border of a narrow but well-devcloped sulcus dentalis along the lingual side of the tooth row; this border is appressed close to the tooth bases, and is shallowly concave opposite several teeth. The shelf ventromedially bears a deep groove for the dorsal edge of the splenial. This groove extends anteriorly and terminates at a point below the sixth tooth position. The anterior end of the shelf bears a blunt but prominent dorsomedial process, forming part of the symphysis. Below the process is a short, fissure-like anterior Meckelian foramen developed under the first six tooth positions. Posteriorly below the deep and robust subdental shelf, the Meckelian canal is open widely, and no splenial is preserved; the Meckelian canal occupies over half of the total depth of the dentary. The lower border of the dentary is a sharp edge, which anteriorly turns medially and upward to the symphysis. On the medial side of the ventral border, a large surface area for the ventral spleniodentary articulation is clearly visible on the specimen, indicating a strong articulation of the two bones along the ventromedial side of the jaw.

The lateral surface of the dentary is flattened, but weakly convex posteriorly. A row of inferior alveolar foramina perforates its dorsal external surface, and the spaces between the foramina obviously increase in length posteriorly. These foramina are

rounded and extremely small in relation to the size of the jaw. The external surface of the dentary is smooth above the foramina, but is heavily ornamented below, with irregular bony rugae. Other specimens show that the external ornamentation is variable in extent, ranging from the ventral edge of the jaw to above the line of mental foramina dorsally. Generally, larger individuals show more extensive ornamentation than smaller ones, implying an increase of ornamentation with age. The dentaries of no other teiids in this study show comparable ornamentation at any size.

The preserved part of the holotype dentary bears 12 teeth and the bases of two others. These teeth are robust and closely spaced, but with slightly recurved, transversely expanded, parallel shafts forming a comb-like dental apparatus; they are subpleurodont, with the parapet of the jaw slightly lower than half of the tooth height (on two well-preserved, smaller specimens, UALVP 29756 and 29913, the parapet is about half the height of the teeth). On the holotype, the first five or six teeth are slightly procumbent, unicuspid, more closely spaced, and more anteroposteriorly compressed than the posterior ones. The teeth posterior to the sixth are bicuspid, with a moderately-sized, rounded accessory cusp developed anterior to the main cusp and set off from it by a clearly-defined groove labially and lingually. In UALVP 29756, the anterior cusp first appears on the ninth tooth; the more anterior teeth are unicuspid with a robust anterior crest running ventrally from the main cusp, and a weaker, shorter apical crest present posteriorly; the crowns are faintly striated lingually. UALVP 29913, with teeth present through the 12th tooth position, shows a distinct anterior crest, but no cusp, on each tooth, although its other dental and mandibular features indicate it pertains to *Glyptogenys*. We interpret these differences to mean that in *Glyptogenys*, the cuspation of the dentary teeth becomes more pronounced with age, as it does in the other teiids included in this study, the reverse of the pattern hypothesizied for *Prototeius* and other teiids by Denton and O'Neill (1995).

On the holotype, the crowns of the posteriormost teeth lean medioposteriorly, and the shafts become increasingly robust posteriorly. The tooth bases are transversely expanded and oriented slightly obliquely across the jaw; in lingual view, they arise from the bone of attachment at a constant height, in contrast to the irregular pattern in *Socognathus*. A ring of cementum is developed around the base of each tooth, and an irregular collar of cementum is developed externally, at the junction between the parapet edge and tooth shafts. The dentary tooth row is incomplete, with probably five to seven posteriormost teeth missing. It is possible when complete specimens are discovered that the posteriormost teeth will prove to be tricuspid or incipiently tricuspid, as the combination of anterior conical with middle bicuspid and posterior tricuspid teeth is common in both extant (e.g., *Crocodilurus* and *Tupinambis*) and fossil teiids (e.g., *Meniscognathus*).

Discussion.—The familial assignment of *Glyptogenys ornata* to the Teiidae is based mainly on the conspicuous deposit of cementum at the tooth bases, and the enlarged splenial, as indicated by the widely open Meckelian canal in the holotype. These are well-recognized synapomorphies of the family Teiidae (MacLean, 1974; Presch, 1974*b*; Estes, 1983*a*; Estes et al., 1988). Another synapomorphy often recognizable on jaw fragments is that the replacement teeth develop posteromedially within subcircular basal cavities (Romer, 1956; Estes et al., 1988). However, this character is in some cases, as on the holotype specimen, unidentifiable as a result of suppression of tooth replacement in adult individuals (MacLean, 1974).

One of the most obvious characters of the holotype is the sculpture on its lateral surface. This sculpture is so pronounced that Gao and Fox (1991) regarded it as taxonomically significant, since sculpture on the lower jaw is not common among modern teiids. In a specimen of *Cnemidophorus* (UMMZ 182042), the lower jaw is ornamented; however, the sculpture on this specimen is developed mostly on the angular bone and is much less rugose than that in *Glyptogenys*. A similar condition is also seen in another extant teiid, *Ameiva* (personal observation). *Cnemidophorus* and *Ameiva* are more closely related to each other than to any of the other genera of the family (Gorman, 1970; Presch, 1974*a*), while *Glyptogenys* shows no feature resembling the two extant genera in terms of jaw shape and tooth form: *Ameiva* and *Cnemidophorus* have a slender mandible with pointed, bicuspid or tricuspid teeth, suitable for feeding on soft-shelled insects, while the deep and robust jaw with thick and bluntly bicuspid teeth in *Glyptogenys* is best designed for prey on hard-shelled beetles or other resistant terrestrial invertebrates. It seems that this character (presence of sculpture on the lateral surface of dentary) has been independently evolved in *Glyptogenys* and in the extant *Cnemidophorus–Ameiva* group.

The osteodermal sculpture on the lower jaw may be ontogenetically variable in extent in lizards. Etheridge (1964) showed ontogenetic development of sculpture on a series of dentaries in *Anolis* iguanids. However, it seems that *Glyptogenys* may represent a different case, because the holotype was probably from a mature but not an old individual (as evidenced by the unworn tooth crowns), but shows extensive ornamentation on the jaw nonetheless. In addition, two small jaw fragments (unnumbered specimens) in the UALVP collection show heavy sculpture, while a larger specimen (UALVP 29756) shows less heavy sculpture. Perhaps the ornamentation in this lizard is sexually dimorphic, but this interpretation is more problematic because of the small sample size of the specimens for this lizard presently available; there is no evidence from modern lizards supporting this interpretation.

Genus *Gerontoseps* Gao and Fox, 1991

Type Species.— *Gerontoseps irvinensis* Gao and Fox, 1991.

Range.—Upper Cretaceous, North America.

Diagnosis.—As for the type and only known species.

Gerontoseps irvinensis Gao and Fox, 1991
(Fig. 13, 14A–D)

Holotype.—UALVP 29754, an anterior part of a right mandible having four teeth and the broken bases of nine others.

Type Locality and Horizon.—Outcrop of the Oldman Formation near Irvine, in Sec. 31, Tp. 11, R 2, W 4, about 40 km east of Medicine Hat, southeastern Alberta; Upper Cretaceous Oldman Formation (Judithian).

Referred Specimens.—UALVP 29757, 29760–29762, 29765–29766, 29768, all incomplete tooth-bearing dentaries. In addition, several unnumbered dentary fragments from the same horizon are also referrable to this speeies.

Known Distribution.—Upper Cretaceous Oldman Formation (Judithian), southeastern Alberta.

Diagnosis (Revised from Gao and Fox, 1991).—A small Late Cretaceous teiid differing from other fossil and extant teiids in having the following combination of character states: mandible shallow but wide, with convex lateral and medial sides; splenial partially fused to dentary in some individuals; sulcus dentalis narrow and conspicuously deep; dentary teeth slightly expanded transversely, with straight-sided shafts; crowns unicuspid, nearly conical, but broad apical cusp having symmetrical anterior and posterior crest; tooth attachment subpleurodont, with lateral parapet about one-third of tooth height.

Description.—The holotype UALVP 29754 (Fig. 13, 14A, B) is an ineomplete right mandible having the splenial partially fused to the dentary. The jaw is relatively shallow, but strong and eonvex both laterally and medially. The lateral eonvexity is probably charaeteristie for this speeies, sinee the lateral surfaee is greatly swollen at a 45-degree angle, and is roughly ">-shaped" in eross section. The medial surfaee has a similar but mueh weaker convexity along the dorsal spleniodentary articulation. The Meckelian eanal is restricted in eomparison to that of *Glyptogenys* and *Socognathus* (see above), but has a wide and horizontal "roof" below the subdental shelf; this wide roof, together with the peeuliar type of eonvexity mentioned above, gives the Meekelian eanal an inverted triangular shape in eross seetion.

In medial view, the subdental shelf is deep anteriorly but sharply reduced posteriorly. The shelf dorsally bears a sharp subdental ridge, which forms the medial border of a narrow but deep sulcus dentalis. Below the shelf, the splenial slightly deepens posteriorly but greatly tapers anteriorly and terminates below the sixth or the seventh anterior tooth. The splenial is dorsally fused to the dentary, along the spleniodentary suture, which is partly reeognizable, but is lost below the seventh and eighth teeth as well as posterior to the 12th tooth position. The ventral spleniodentary artieulation remains unfused, and is located medially along the ventral border of the jaw.

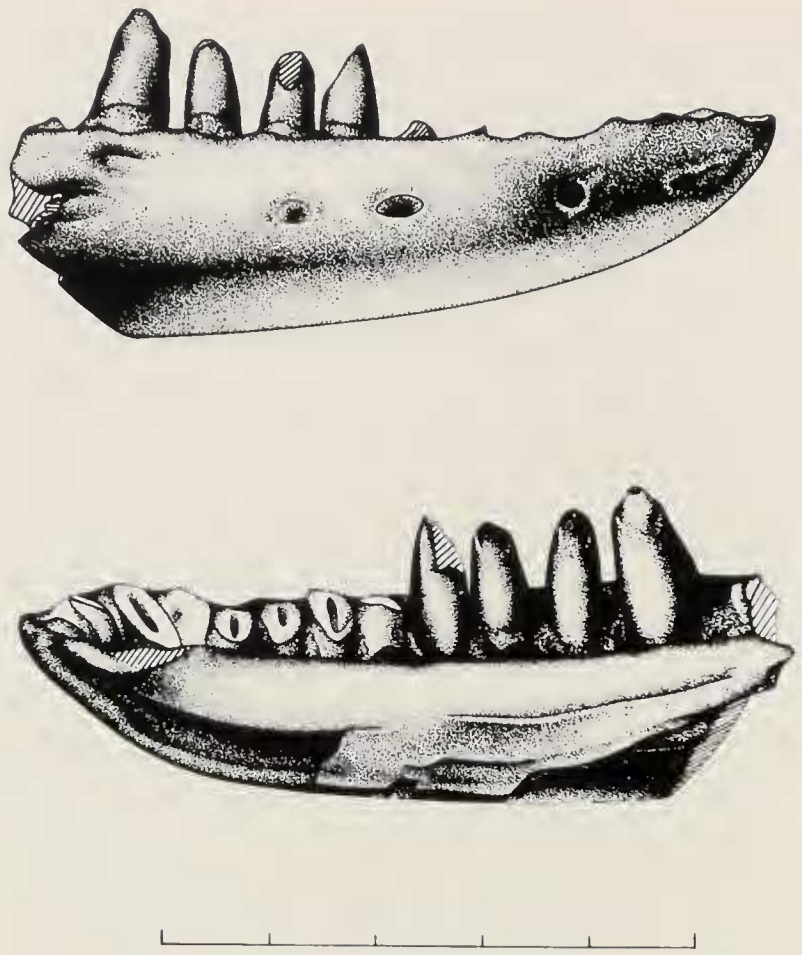

Fig. 13.—*Gerontoseps irvinensis,* Oldman Formation, Alberta: UALVP 29754 (holotype), ineomplete right mandible, lateral (above) and medial (below) views. Seale = 5 mm.

The holotype shows the anteriormost 13 tooth positions of the jaw, ineluding four teeth (three eomplete) and the broken bases of nine others. The anterior six or seven teeth are slightly compressed anteroposteriorly, but the middle and posterior teeth are increasingly eolumnar, swollen, and widely spaced. Tooth attaehment is subpleurodont, with the lateral parapet as low as one-third of the tooth height. The erowns are bluntly unieuspid and nearly conieal, but have symmetrieal anterior and posterior ridges. The basal deposit of eementum is less heavy than in *Glyptogenys* and *Socognathus.* Replacement pits are developed posteromedially at the base of the eighth and tenth teeth.

Among the referred specimens, UALVP 29760–29761 (Fig. 14C, D) are better preserved than the others. These specimens clearly show the same kind of tooth form as the holotype, but the fusion of the splenial to the dentary is not developed. The two speeimens have 13 or 14 dentary teeth preserved, but are broken at or in front of the posterior interior alveolar foramen. This gives an indication that the total tooth eount of *Gerontoseps* is approximately 18 on the dentary, sinee the number of tooth positions posterior to the foramen is usually four to five in teiids (personal obscrvation).

Discussion.—Perhaps the most obvious feature of the holotype (UALVP 29754) is the fusion of the splenial with the dentary along the dorsal spleniodentary suture. Gao and Fox (1991) interpreted this fusion on the holotype as taxonomically significant,

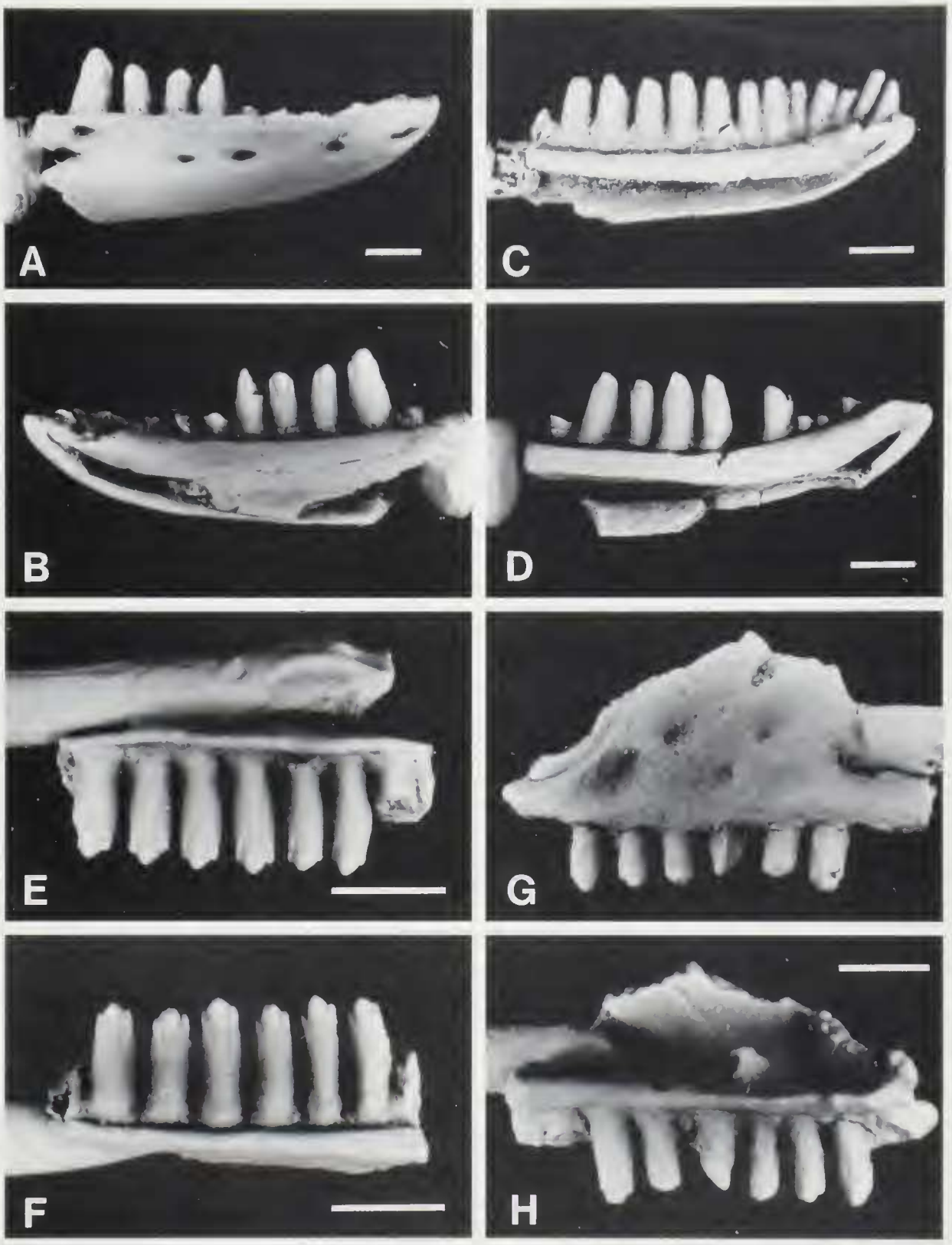

Fig. 14.—*Gerontoseps irvinensis,* Oldman Formation, Alberta: A, B, UALVP 29754 (holotype), incomplete right mandible, lateral and medial views; C, UALVP 29760, left dentary, medial view; D, UALVP 29761, left dentary, medial view. *Leptochamops denticulatus,* Frenchman Formation, Saskatchewan: E, SMNH P1927.231, fragmentary left maxillary, medial view; F, SMNH P1927.893, fragmentary left dentary, medial view; G, H, SMNH P2004.89, left maxillary, lateral and medial views. Scale = 1 mm.

owing to the small size of the specimen and the low probability that such extensive fusion would occur in such a young individual. Now with more specimens in the collection, the fusion appears to be individually variable. The holotype probably represents a mature individual, in spite of its small size and unworn tooth crowns. This type of fusion is obviously different from the homoplastic enclosure of the Meckelian canal in iguanids (Etheridge and de Queiroz, 1988), gymnophthalmids (MacLean, 1974), some scincids (Greer, 1970), xantusiids, and amphisbaenians (Gans, 1978), because the conditions in the latter groups are all associated with splenial reduction, while the splenial in *Gerontoseps* is large. The deep sulcus dentalis, well-defined subdental shelf, large splenial, and subpleurodont den-

tition are all consistent with classification of *Gerontoseps* in the Teiidae.

Spleniodentary fusion is also known in the Lancian teiid *Haptosphenus* (see Estes, 1964; see also description below), but *Gerontoseps* is substantially different from the latter in other aspects of jaw construction and tooth form. The dentary teeth of *Gerontoseps* are basically conical (although having symmetrical side ridges), and show no tendency towards developing a tricuspid or incipiently tricuspid crown pattern. Instead, the bluntly unicuspid teeth of *Gerontoseps* increase in size posteriorly, showing a tendency to develop into enlarged cheek teeth. These features, combined with the shortness of the jaw and partial spleniodentary fusion, indicate a crushing function. Perhaps this lizard had a food preference for small hard-shelled insects.

Genus *Leptochamops* Estes, 1964

Type Species.—*Chamops denticulatus* Gilmore, 1928.

Range.—Upper Cretaceous, North America.

Diagnosis (Revised from Estes, 1983a).—A Late Cretaceous teiid broadly related to the extant *Kentropyx–Cnemidophorus–Ameiva* group, sharing with the group derived character states such as having the dentary tooth row curved corresponding to the lateral curvature of the dentary; differing from the group in having higher-crowned teeth, which are uniformly tricuspid or incipiently tricuspid, except for anterior teeth, which are unicuspid; probably more closely related to *Meniscognathus* Estes, 1964, but differing from the latter genus in having a combination of the following character states: subdental shelf narrow and strongly dorsoventrally concave; marginal teeth high-crowned, having cylindrical shaft and tricuspid or incipiently tricuspid crown pattern; tooth attachment subpleurodont, having lateral parapet about one-half to one-third of tooth height.

Leptochamops denticulatus (Gilmore, 1928) Estes, 1964
(Fig. 14E–H)

Holotype.—YUM 1062, nearly complete left dentary with 23 teeth, collected by J. B. Hatcher in 1889 (see Gilmore, 1928). The same specimen was later cited as USNM 16514 (see Estes, 1964).

Type Locality and Horizon.—"Peterson's quarry," Lance Creek, Niobrara County, eastern Wyoming; Upper Cretaceous Lance Formation (Lancian).

Referred Specimens.—SMNH P1927.231, P1927.871, P1927.908, P2004.89, fragmentary maxillaries; SMNH P1927.872, P1927.893, P2004.129, fragmentary dentaries.

Locality and Horizon.—Gryde locality, in Sec. 19, Tp. 14, R 18, W 3, Frenchman River valley, southwestern Saskatchewan; Upper Cretaceous Frenchman Formation (Lancian).

Known Distribution.—Upper Cretaceous Lance Formation, eastern Wyoming; Hell Creek Formation, eastern Montana; Frenchman Formation, southwestern Saskatchewan (all Lancian).

Diagnosis.—A species of *Leptochamops* differing from *L. thrinax* Gao and Fox, 1991 in having the middle and posterior dentary teeth weakly or only incipiently tricuspid, more closely spaced; marginal tooth row strongly curved, corresponding to stronger facial constriction; subdental shelf more slender and dorsoventrally concave.

Description.—The referred specimens include four maxillaries and three dentaries, all collected from the Gryde locality (see Storer, 1991) in the Frenchman Formation. Among these specimens, two (SMNH P1927.231, P1927.893) are better preserved than the others in terms of showing tooth morphology. SMNH P1927.231 (Fig. 14E) is the posterior part of a left maxillary, with six complete teeth and the base of another. Although fragmentary, the well-preserved teeth are characteristically of *Leptochamops denticulatus* type: cylindrical, high crowned, slender, and tricuspid posteriorly in the tooth row. Tooth attachment is subpleurodont, with a low lateral parapet of the maxillary being less than one-half of the tooth height. In medial view, the supradental shelf is much more slender than in *Chamops*, but similar to that of *Meniscognathus* from the same horizon. In ventral view, the posterior narrowing of the shelf indicates that the specimen is broken close to the end of tooth row, with probably only one posteriormost tooth missing.

The other better preserved specimen (SMNH P1927.893, Fig. 14F) consists of a fragmentary left dentary containing six posterior teeth. The subdental shelf is slender, differing from that in *Chamops*. This specimen is too fragmentary to show the dentary structure of this lizard, but the teeth preserved resemble those in SMNH P1927.231 in cusp pattern and the mode of attachment.

Discussion.—Gilmore (1928) founded "*Chamops denticulatus*" on several jaws from the Lance Formation. The holotype (YUM 1062), a complete left dentary containing 23 teeth, was the specimen originally assigned to *Chamops segnis* as one of the "dentary bones with precisely similar teeth, and corresponding in size with the jaws figured" (Marsh, 1892:450). Gilmore (1928) placed "*Chamops denticulatus*" in the Iguanidae*. This familial assignment was based largely on Camp's (1923) comments on form and attachment of the teeth in *Chamops segnis*, which included the specimens of the then-unrecognized *Chamops denticulatus*. Estes (1964) revised Gilmore's "*Chamops denticulatus*" by referring it to the new genus *Leptochamops*. The

holotype that Estes cited as USNM 16514 is the very same specimen as Gilmore's YUM 1062. The change of the specimen number was apparently a result of an exchange of specimens between Yale and the Smithsonian Institution in the early 1920s (M. A. Turner, personal communication, 1989). Estes (1964) confirmed the affiliation of *L. denticulatus* with the Teiidae, and later (Estes, 1983*a*) pointed out its possible relationships with the living *Kentropyx–Cnemidophorus–Ameiva* group, on the resemblance in curvature of the tooth row.

Leptochamops denticulatus is definitely known only from the Lance, Hell Creek, and the Frenchman formations (all Lancian in age). The same species has been reported from pre-Lancian horizons in Montana and New Mexico, but these reports are either unconvincing or simply based on misidentified specimens, as discussed below:

1) Sahni (1972) identified two specimens (AMNH 8490–8491) as *Leptochamops denticulatus* and stated that "the Judith River material of *Leptochamops denticulatus* is identical to that from the Lance Formation" (Sahni, 1972:353). AMNH 8490 is a dentary fragment with two teeth preserved (personal observation). The teeth are high crowned, cylindrical, and appear to be incipiently tricuspid; however, lack of information on jaw structure prevents referral of the specimen to this particular species, although there seems to be little doubt about its association with *Leptochamops*. The other specimen (AMNH 8491; see Sahni, 1972:fig. 8K) is a maxillary fragment with seven teeth. These teeth are low crowned and slightly recurved rather than procumbent; comparison should be made to those of *Meniscognathus*.

Until this study, the maxillary structure of *Leptochamops* was poorly known, but SMNH P2004.89 (Fig. 14G, H) and UALVP 29746 (a comparative specimen from the Lance Formation) show a slender premaxillary process and relatively low facial process, as in the extant *Cnemidophorus* (see Presch, 1970). The teeth preserved on these maxillaries are clearly of the *L. denticulatus* type, as they are high crowned, cylindrical, and have an incipiently tricuspid crown pattern. AMNH 8491 lacks these features (personal observation) and shows no significant resemblance to Lancian *Leptochamops denticulatus* in terms of tooth form or jaw configuration. Therefore, AMNH 8491 would be better referred to as "Teiidae, gen. et sp. indet.," if its affiliation with *Meniscognathus* cannot be confirmed.

2) Armstrong-Ziegler (1978), in a faunal list, reported the occurrence of *Leptochamops denticulatus,* together with *Chamops segnis,* from the Fruitland Formation, New Mexico. Subsequently, the same author (1980), in a descriptive paper, referred six jaw fragments (UALP 75137D, E, K–N) to *Leptochamops denticulatus*; and this identification was accepted in Estes' (1983*a*) review of fossil lizards. Unfortunately, some of these specimens appear to have been anatomically and taxonomically misidentified. A "dentary" (UALP 75137D, see Armstrong-Ziegler, 1980:pl. 2d) is neither a dentary nor from a lizard; instead, the photograph of the specimen clearly shows a premaxillary of *Albanerpeton,* an aberrant amphibian previously thought to be a prosirenid salamander (see Fox and Naylor, 1982; McGowan and Evans, 1995). The original description of UALP 75137K stated that "many of the tooth crowns have a black shaft capped by a sharply contrasting light brown occlusal surface" (Armstrong-Ziegler, 1980:18). This description and the photograph of UALP 75137D give a clear picture of the teeth of *Albanerpeton* rather than those of a lizard. Two other specimens (UALP 75137M, N), have "bicolored teeth that extend about one-half their height over the parapet of the deep dorsoventral border of the bone" (Armstrong-Ziegler, 1980:20); these may be also referrable to *Albanerpeton,* although some specimens of *L. denticulatus* retain a band of black pigment between the shaft and crown (Estes, 1964:112). The specimen UALP 75137E was neither described nor figured in Armstrong-Ziegler's paper.

Consequently, at least one of the specimens from the Fruitland Formation has been misidentified, and various doubts attend the others, even "the most complete and diagnostic dentary" (UALP 75137K, Armstrong-Ziegler, 1980:18), if only because the latter has not been figured. The identification of AMNH 8490–8491 as *Leptochamops denticulatus* is unconvincing; and hence, the occurrence of the species in the Judith River Formation, Montana, is questionable. Several specimens of pre-Lancian *Leptochamops* are known from the Oldman Formation, but cannot be assigned to the Lancian species *L. denticulatus* with certainty (see later discussion).

Leptochamops thrinax Gao and Fox, 1991
(Fig. 15, 16A–D)

Holotype.—UALVP 29749, incomplete left dentary having five teeth and bases of ten others.

Type Locality and Horizon.—Outcrop of the Oldman Formation near Irvine, in Sec. 31, Tp. 11, R

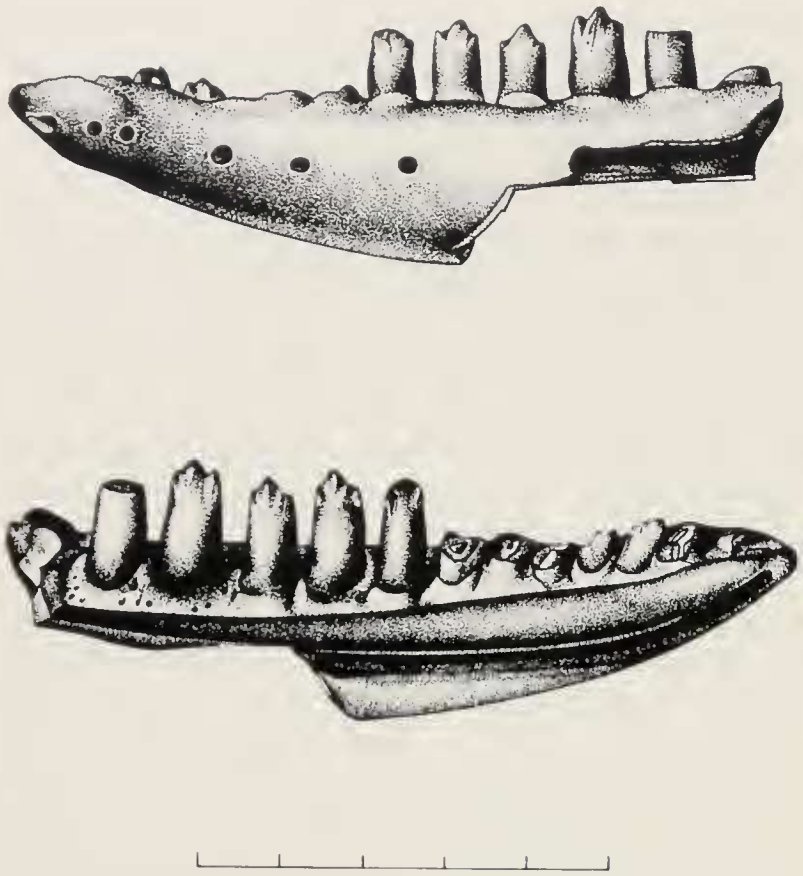

Fig. 15.—*Leptochamops thrinax*, Oldman Formation, Alberta: UALVP 29749 (holotype), incomplete left dentary, lateral (above) and medial (below) views. Scale = 5 mm.

2, W 4, about 40 km east of Medicine Hat, southeastern Alberta; Upper Cretaceous Oldman Formation (Judithian).

Referred Specimens.—UALVP 29748, 29750, 29753; all topotypic dentary fragments having several teeth preserved.

Known Distribution.—Upper Cretaceous Oldman Formation (Judithian), southeastern Alberta.

Diagnosis (after Gao and Fox, 1991).—A Judithian species of *Leptochamops* differing from the Lancian *Leptochamops denticulatus* in having the dentary teeth broadly tricuspid, widely spaced, more robust, and fewer in number; subdental shelf relatively straight and stronger; and Meckelian canal more restricted.

Description.—The holotype, UALVP 29749 (Fig. 15, 16A, B), is long and slender, gently tapering anteriorly and having a pointed anterior end. Medially, the dentary bears a relatively strong subdental shelf, which abruptly diminishes in depth posteriorly, in contrast to the gentle reduction in depth seen in *Leptochamops denticulatus*. The shelf is relatively straight by comparison, curving only weakly dorsally at its anterior end. The dorsal ridge of the shelf is low, medially bordering a narrow and shallow sulcus dentalis along the tooth bases. The Meckelian canal takes up about half the depth of the dentary, and thus is more restricted than in *L. denticulatus*, indicating a more narrow splenial. The dorsal groove and the ventral surface for the splenioclentary articulation imply that the splenial terminates under the seventh anteriormost tooth position, leaving a long, fissure-like anterior Meckelian foramen. The mandibular symphysis is weakly built. Laterally, the external surface of the dentary is smooth, and is more convex posteriorly than anteriorly. Seven inferior alveolar foramina can be seen on the holotype, but other specimens, such as UALVP 29748 and 29753 (Fig. 16C, D), show that the number and arrangment of these foramina are individually variable.

The holotype bears five teeth and the bases of ten others. The teeth are high-crowned, cylindrical, widely spaced, and subpleurodont in their mode of attachment. The tooth crowns, slightly tipped lingually, are broadly tricuspid, having a prominent central cusp and two much less prominent accessory cusps; the apices of some teeth are heavily striated labially and lingually. The anterior cusp is stronger and more clearly separated from the main cusp than the posterior accessory cusp. The complete tooth count for this species is estimated as 16–17, on the basis of the termination of the subdental shelf (the tooth row usually ends slightly anterior to where the subdental shelf meets the coronoid). In dorsal view, the tooth row is relatively straight, lacking the characteristic curvature seen in the Lancian species *L. denticulatus* and *Meniscognathus altmani* Estes, 1964. The tooth bases are surrounded with a deposit of cementum, as commonly seen in other fossil teiids.

Discussion.—The holotype, UALVP 29749, shows several taxonomically significant characters, including long and slender dentary, weak symphysis, restricted Meckelian canal, and straight, cylindrical, high-crowned teeth, that distinguish this lizard from other teiids from the Oldman Formation, including *Socognathus* and *Gerontoseps*. On the basis of these same features, Gao and Fox (1991) referred this lizard to *Leptochamops*, distinguishing it from the Lancian *L. denticulatus*. When compared to the latter species, its nearly straight subdental shelf, strongly tricuspid and widely spaced dentary teeth, and nearly straight tooth row indicate differences at the specific level.

Several other specimens from the same formation show character states that more closely resemble *L. denticulatus* than *L. thrinax* (see discussion below), suggesting that the above-mentioned differences may be generically significant. Indeed, if the primitive condition for the dentition of *Leptochamops* and the closely related *Kentropyx–Cnemidophorus–Ameiva* group is to have incipiently tricuspid teeth, the Judithian *L. thrinax* with broadly tricuspid teeth may be less closely related to *L. denticulatus* than Gao and Fox (1991) thought. However, current understanding of *L. thrinax* is not yet sufficient to separate it from the Lancian *L. denticulatus* at the generic level.

Leptochamops sp., cf. *L. denticulatus* (Fig. 16E, F)

Referred Specimens.—UALVP 29741, 29772, right dentaries each having 16 tooth positions preserved.

Locality and Horizon.—Outcrop of the Oldman

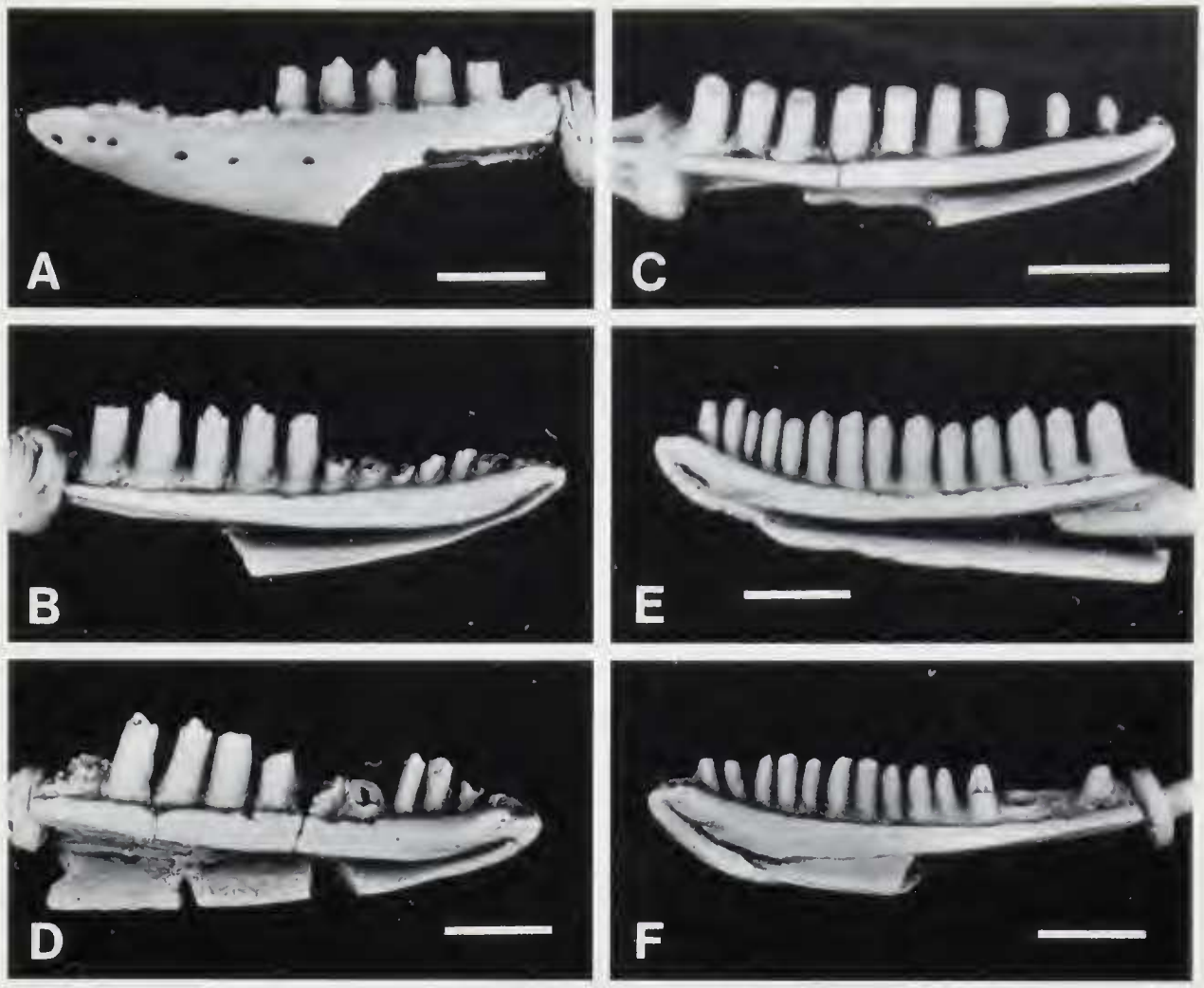

Fig. 16.—*Leptochamops thrinax,* Oldman Formation, Alberta: A, B, UALVP 29749 (holotype), lateral and medial views; C, UALVP 29748, left dentary, medial view; D, UALVP 29753, left dentary, medial view. *Leptochamops* sp., cf. *L. denticulatus,* Oldman Formation, Alberta: E, UALVP 29772, nearly complete right dentary, medial view; F, UALVP 29741, right dentary with partial splenial, medial view. Scale = 2 mm.

Formation near Irvine (for legal description, see above).

Description.—The specimen UALVP 29772 (Fig. 16E) is a nearly complete right dentary having 14 complete teeth and the bases of two others. Medially, as in the Lancian *Leptochamops denticulatus,* the dentary bears a slender but well-defined subdental shelf. The shelf curves upwards anteriorly and gently diminishes posteriorly, differing from *L. thrinax,* in which the shelf is straight and abruptly decreases posteriorly. The splenial is missing as a consequence of preservation, leaving the Meckelian canal open proportionally as widely as that in *L. denticulatus.* On the ventral side of the subdental shelf, the groove for the dorsal spleniodentary articulation indicates that the splenial terminated anteriorly below the sixth anteriormost tooth, leaving a narrow opening for the Meckelian canal facing downwards and medially. The splenial does not cross over the ventral midline, and thus is located entirely on the medial side of the jaw.

The lateral surface of the dentary is more convex posteriorly than anteriorly, but is not strongly swollen near the dentary–coronoid articulation. The seven interior alveolar foramina on UALVP 29772 represent the total number for this lizard. The first six foramina are small, closely spaced, and located below the first ten teeth; a gap then separates these foramina from the seventh, under the 13–14th teeth. In dorsal view, the lateral surface of the dentary is curved as in *L. denticulatus,* with the middle part of the jaw being slightly concave.

The tooth row on UALVP 29772 is incomplete, with probably two or three posterior teeth missing. The first two teeth are broken, with only the tooth bases preserved. The next 14 teeth are complete, and are subpleurodont in their mode of attachment. The first seven are conical and their bases are more anteroposteriorly compressed than those that follow. All of the other teeth are incipiently tricuspid, having a blunt central main cusp, which is slightly tipped medially, with poorly defined side "cusps" or "ridges." The posterior teeth are basically cylindrical, but are slightly concave lingually. No replacement pits are evident on this specimen. The basal deposit of cementum is much less heavy than that of *Chamops, Socognathus,* and the holotype of *Leptochamops denticulatus.* A sulcus dentalis is well developed along the medial side of the tooth row, and is deeper anteriorly than posteriorly. The tooth row is curved in accordance with the curvature of the dentary.

Another specimen, UALVP 29741 (Fig. 16F), is a tooth-bearing right dentary broken directly behind the 16th tooth position. The splenial on this specimen has its anteriormost part still attached to the dentary, but the posterior part is broken off, as in most fossil teiid specimens. Although the crowns of most of the teeth are partially dissolved, the anterior teeth closely resemble those of UALVP 29772. This character, plus the high-crowned teeth and curvature of the tooth row, indicate that this specimen is also referrable to "*Leptochamops* sp., cf. *L. denticulatus.*"

Discussion.—The specimens UALVP 29741 and

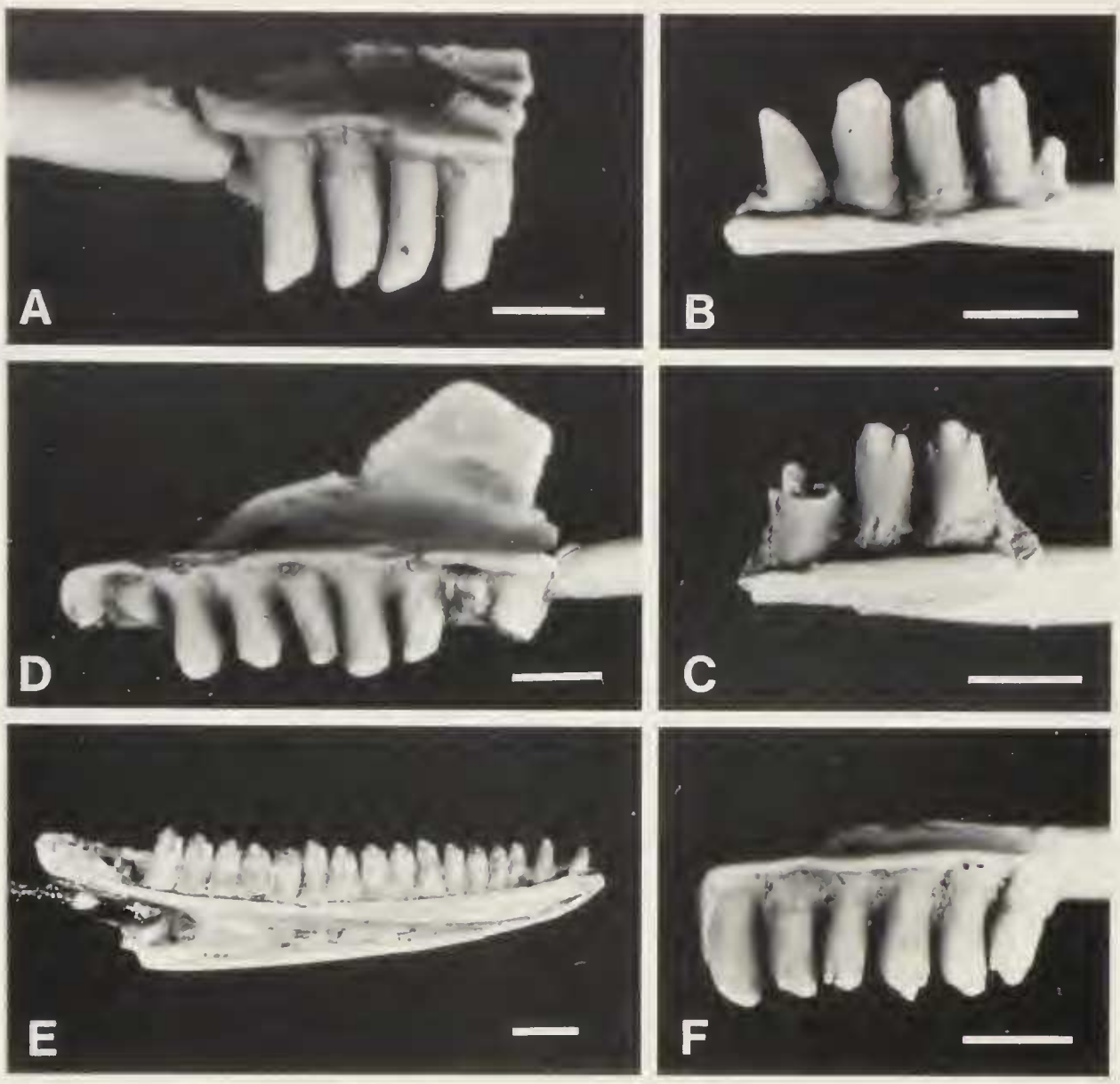

Fig. 17.—*Meniscognathus altmani,* Frenchman Formation, Saskatchewan: A, SMNH P1927.900, left maxillary fragment, medial view; B, SMNH P1927.903, right dentary fragment, medial view; C, SMNH P1927.887, left dentary fragment, medial view; D, UALVP 29833, left maxillary, medial view; Lance Formation, Wyoming: E, UALVP 29774, nearly complete left dentary, medial view; Hell Creek Formation, Montana: F, UALVP 29775, right maxillary fragment, medial view. Scale = 1 mm.

29772 represent a Judithian teiid that is closely related to the Lancian *Leptochamops denticulatus.* The curved dentary and tooth row, dorsally concave subdental shelf, and incipiently tricuspid crown pattern all are different from *Leptochamops thrinax* from the same horizon, but resemble the Lancian *L. denticulatus* as revised by Estes (1964). On the basis of these character states, these two specimens are referred to *Leptochamops,* close to the type species. However, the differences, such as less high-crowned and fewer dentary teeth, much weaker cuspidation, and less heavy basal deposit of cementum on UALVP 29741 and 29772, may indicate separation at a species level from *L. denticulatus.* It appears that the two specimens from the Oldman Formation represent a species that is more closely related to *L. denticulatus* than to *L. thrinax,* which has broadly tricuspid teeth and a straighter jaw.

Genus *Meniscognathus* Estes, 1964

Type Species.—*Meniscognathus altmani* Estes, 1964.

Range.—Upper Cretaceous, North America.

Diagnosis.—As for the type and only known species.

Meniscognathus altmani Estes, 1964 (Fig. 17)

Holotype.—UCMP 46610, complete left dentary with 13 teeth and the broken bases of 15 others.

Type Locality and Horizon.—Lull 2 quarry (UCMP loc. V-5620), Lance Formation, Niobrara County, eastern Wyoming (Clemens, 1963; Estes, 1964).

Referred Specimens.—Frenchman Formation, Gryde locality: SMNH P1927.900, P1927.918, P1927.960, P1927.999, P2004.91

(total: five), incomplete maxillaries; SMNH P1927.887, P1927.895, P1927.903, P1927.915 (total: four), fragmentary dentaries. Wounded Knee locality: UALVP 29833, fragmentary maxillary. Lance Formation, BTB locality (UCMP loc. V-5711): UALVP 29832, maxillary; UALVP 29774, 29777, 29834, dentaries. Hell Creek Formation, BCA locality: UALVP 29775, 29779, maxillaries; UALVP 29776, 29831, dentaries.

The BTB and BCA specimens from outside of the study area are included here, because the BCA specimens document the first occurrence of this species in the Hell Creek Formation, and the BTB specimens show significant variation in tooth form that was not clearly known before.

Known Distribution.—Upper Cretaceous Lance Formation, eastern Wyoming; Hell Creek Formation, eastern Montana; Frenchman Formation, southwestern Saskatchewan (all Lancian).

Diagnosis (Revised from Estes, 1983a).—A Late Cretaceous teiid differing from the closely related *Leptochamops* in having a dentary more slender and more delicately built; dentary teeth short, laterally compressed, and medially concave; tooth crowns broadly bicuspid or weakly tricuspid; tooth attachment pleurodont, with about two-thirds of tooth height attached to lateral parapet of jaw. Differing from extant *Kentropyx* and related forms in having the marginal teeth low crowned, less lingually concave, with blunter cusps.

Description.—Most of the referred specimens from the Frenchman Formation are too fragmentary to show details of jaw structure, but preserved teeth show taxonomically significant features on which the referral of these specimens is based. SMNH P1927.900 (Fig. 17A) is a fragmentary left maxillary from the Gryde locality. Although fragmentary, the specimen has four teeth preserved, and these show diagnostic features of *Meniscognathus altmani,* being low crowned, medially concave, slightly recurved, and closely spaced. The four teeth are bicuspid and are not strongly compressed labiolingually, as they represent the middle part of a maxillary tooth row (comparable with those on the middle part of the holotype dentary, see Estes, 1964:fig. 53). These teeth are pleurodont, with about two-thirds of their height attached to the lateral parapet of the maxillary.

SMNH P1927.903 (Fig. 17B) is a dentary fragment, with four teeth preserved. Differing from the fragmentary maxillary described above, the teeth on this specimen are tricuspid, laterally compressed, and less recurved. These features, in keeping with the slender subdental shelf, indicate that the four teeth are from the posterior part of tooth row. Teeth on another dentary fragment, SMNH P1927.887 (Fig. 17C), also a posterior part, show a similar morphology. Six other specimens (SMNH P1927.895, P1927.915, P1927.918, P1927.960, P1927.999, and P2004.91) from the Gryde locality are more fragmentary than the three described above, but from their similar tooth form, are clearly referrable to the same species.

UALVP 29833 (Fig. 17D) is the posterior part of a left maxillary from the Wounded Knee locality of the Frenchman Formation. The maxillary fragment has nine tooth positions, including five teeth and the broken bases of four others. The five teeth are not well preserved, but still show the distinctive features of *Meniscognathus,* as they are low crowned, laterally compressed, medially concave, and tricuspid.

The specimen UALVP 29774 (Fig. 17E) from the BTB locality is a nearly complete left dentary, which displays details of the jaw structure and retains the complete tooth count of this teiid (see below). As in the holotype (UCMP 46610), the dentary is more delicately built than that of *Leptochamops denticulatus.* The teeth on this dentary are pleurodont, having about one-third of their height projecting above the lateral parapet. These teeth are low crowned, closely spaced, and the tooth row is slightly curved corresponding to the lateral curvature of the dentary. In contrast to the holotype, which shows 28 tooth positions, there are a total of 21 in this specimen, including 16 teeth and tooth bases, as well as spaces for five others. The anterior seven teeth are conical, followed by six bicuspid and then eight posterior weakly tricuspid teeth. The bicuspid teeth in the middle part of the tooth row have the crowns bearing a prominent posterior main cusp and a smaller but clearly defined anterior accessory cusp. The posterior teeth have a weak posterior accessory cusp, leaving the crowns only weakly tricuspid. Unlike the corresponding teeth in the holotype, these teeth are mostly straight, although some (8–10, 12, and 14) are slightly recurved. The short tooth shafts are anteroposteriorly compressed for the anterior conical teeth, but increasingly laterally compressed and lingually concave from the middle bicuspid to the posterior tricuspid teeth. The basal deposit of cementum for the dentary teeth is much less heavy than in *Chamops* and *Leptochamops,* as well as other Lancian teiids. A narrow sulcus dentalis is clearly recognizable above the subdental shelf and medial to the tooth row.

In the UALVP collections, four specimens document the first record of *Meniscognathus altmani* from the Hell Creek Formation, eastern Montana. These specimens are: UALVP 29775 (Fig. 17F), a right maxillary fragment with six well-preserved teeth; UALVP 29776, anterior part of a right dentary with four teeth and bases of six others; UALVP 29779, an incomplete left maxillary with 12 badly worn teeth; and UALVP 29831, an incomplete right dentary having five teeth plus bases and spaces for ten others. All of these specimens show a tooth morphology comparable to those from the type Lance Formation (see Estes, 1964: fig. 53), and are clearly referrable to *M. altmani.* One of the specimens (UALVP 29779) has heavily worn and eroded crowns, but still shows significant features, such as low-crowned, pleurodont, medially concave teeth forming a curved tooth row.

Discussion.—Meniscognathus altmani has been previously reported only from the Upper Cretaceous Lance Formation of eastern Wyoming (Estes, 1964, 1983*a*), but not from the Hell Creek Formation of eastern Montana (Estes et al., 1969; Estes and Berberian, 1970). The new specimens reported here from the Hell Creek Formation (BCA locality) and the Frenchman Formation (Gryde and Wounded Knee localities) represent the first discoveries of this teiid from Late Cretaceous deposits other than the Lance Formation. These discoveries indicate that *Meniscognathus altmani* is a widely distributed Lancian teiid, like *Leptochamops denticulatus,* in the Western Interior of North America.

A problem with *Meniscognathus altmani* as described by Estes (1964) concerns the number of

marginal teeth. The species was originally diagnosed as "a teiid lizard with from twenty-one to twenty-eight dentary and about twenty-two (in the only complete specimen) maxillary teeth. . ." (Estes, 1964:113). Probably realizing that the tooth count alone is a nondiagnostic feature for most lizard species, Estes (1983*a*) eliminated the above-cited character from the revised diagnosis, but it remained in the description. The tooth count of this lizard ranges from 21 to 28, unexpectedly wide for a teiid from present understanding of variation in the living species of the group. The normal range of individual variation in extant teiid species is no more than five positions (Edmund, 1969), mostly around three. Perhaps *Meniscognathus altmani* is exceptional among teiids with the tooth count varying more than in other species. The nearly complete dentary described above (UALVP 29774) has 21 tooth positions in a full tooth row. Its low number of teeth, in keeping with the relatively straight tooth shafts and more delicately built dentary, is suggestive of an alternative interpretation: the subdivision of the "21-phenon" (term "phenon" sensu Mayr and Ashlock, 1991) with straight teeth and the "28-phenon" with recurved teeth may indicate that this lizard is sexually dimorphic in terms of tooth count and curvature. However, current sample size and poor preservation of most specimens known for this taxon are not sufficient to demonstrate this alternative interpretation.

Another problem with *Meniscognathus altmani* concerns the morphology of the crowns of the marginal teeth. The species was first diagnosed as having broadly tricuspid crowns (Estes, 1964), but later revised as having "broadly triconodont or bicuspid crowns" (Estes, 1983*a*:91). The holotype (UCMP 46610) shows that only the posterior teeth are weakly tricuspid, the middle teeth are bicuspid, while the anterior ones have been broken away. Estes' "broadly tricuspid" characterization was based on a fragmentary maxillary (UCMP 46081) bearing six posterior teeth. The newly discovered dentary, UALVP 29774, in comparison with two other well-preserved specimens known for this teiid (UCMP 46610, 54266), indicates that the anterior teeth of this species are conical, the middle bicuspid, and the posteriormost weakly tricuspid. The diagnosis for this lizard has been revised accordingly.

Among Lancian teiids, *Meniscognathus* is closely related to *Leptochamops* (Estes, 1964, 1983*a*), and the two together can be placed in the Teiinae (sensu Presch, 1983), as evidenced by their resemblances to the extant *Kentropyx–Cnemidophorus–Ameiva* group in tooth morphology and jaw structure (Estes, 1983*a*). In regard to jaw shape and tooth form, this group is generally characterized by having a shallow, slender, and elongated dentary in comparison with the closely related Tupinambinae, and in having the combination of anterior conical + middle bicuspid + posterior tricuspid teeth, as described here.

Genus *Haptosphenus* Estes, 1964

Type Species.— Haptosphenus placodon Estes, 1964.

Range.—Upper Cretaceous, North America.

Diagnosis.—As for the type and only known species.

Haptosphenus placodon Estes, 1964
(Fig. 18)

Holotype.—UCMP 46035, a nearly complete right dentary with 16 tooth positions (the specimen number is misprinted as 46305 in Estes, 1964:116).

Type Locality and Horizon.—Lull 2 quarry (UCMP loc. V-5620), "near the head of a tributary of Buck Creek," Lance Formation, Niobrara County, eastern Wyoming (Clemens, 1963:23; Estes, 1964).

Referred Specimens.—Frenchman Formation, Gryde locality: SMNH P1920.23, left mandible; Wounded Knee locality: UALVP 29771, 29780, incomplete mandibles. Scollard Formation, KUA-1 locality: UALVP 33921, incomplete mandible.

Known Distribution.—Upper Cretaceous Lance Formation, eastern Wyoming; Hell Creek Formation, eastern Montana; Frenchman Formation, southwestern Saskatchewan; and Scollard Formation, central Alberta (all Lancian).

Diagnosis (Revised from Estes, 1964).—A Late Cretaceous teiid characterized by the following combination of character states: mandible short and robust, with extensive fusion of splenial, coronoid, dentary and surangular bones; splenial strongly notched anteriorly; dentary teeth low crowned, laterally compressed, and bluntly tricuspid; sulcus dentalis lost; tooth attachment subacrodont, with lateral parapet remaining less than one-third of tooth height.

Description.—SMNH P1920.23 (Fig. 18A) from the Gryde locality, Frenchman Formation, consists of an incomplete left mandible (most of the dentary with splenial), which is broken just behind the 13th tooth position. Tapering upward anteriorly, the jaw is short, robustly built, and has the same configuration as the holotype (UCMP 46035).

Medially, the dentary bears a weak process at its anterior end, forming the main part of the weak mandibular symphysis. The

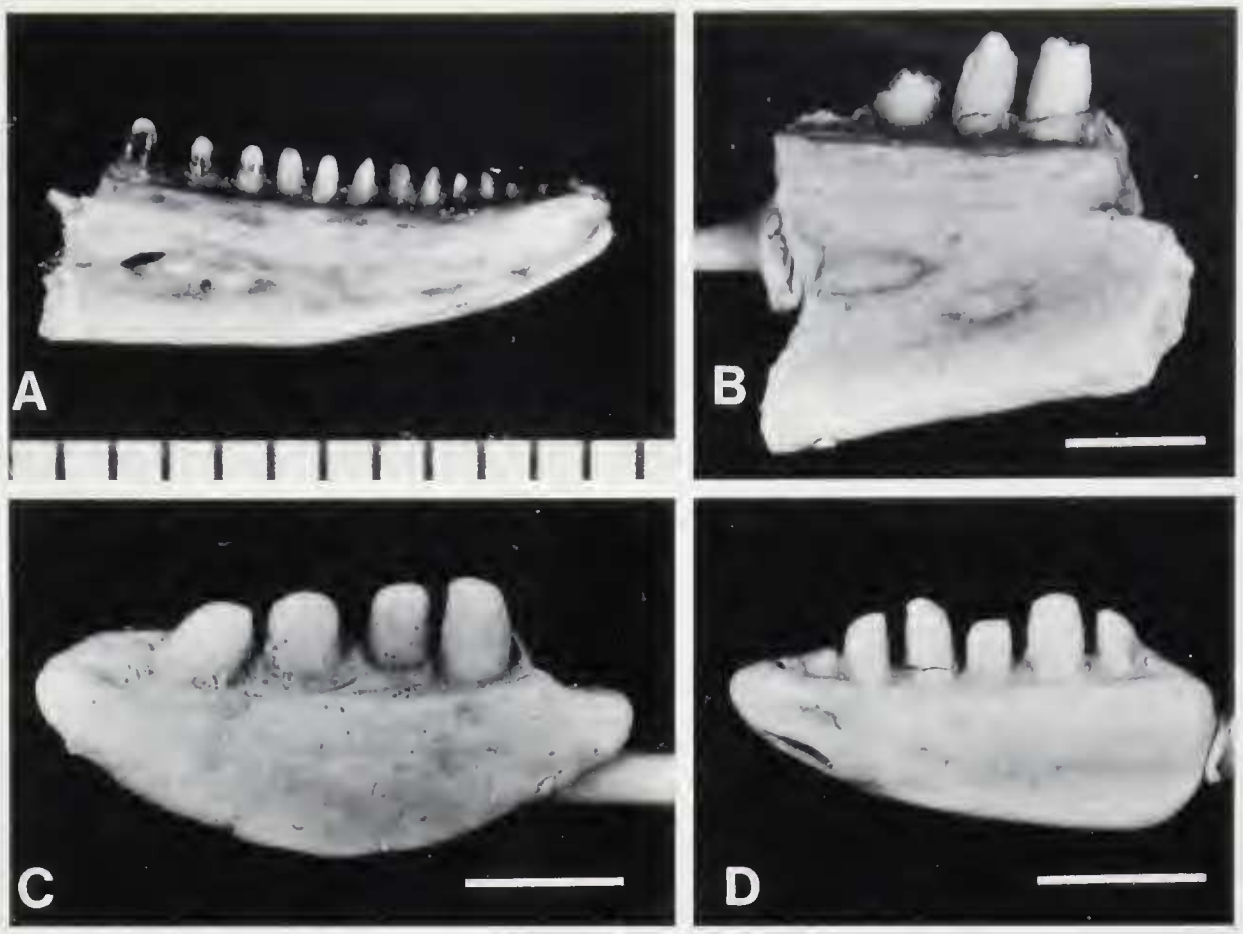

Fig. 18.—*Haptosphenus placodon,* Frenchman and Scollard formations, Saskatchewan and Alberta: A, SMNH P1920.23, left mandible, medial view; B, UALVP 33921, fragment of left mandible, medial view; C, UALVP 29771, fragment of right mandible, medial view; D, UALVP 29780, fragment of right mandible, medial view. Scale divisions for A = 1 mm; scale for B–D = 2 mm.

large splenial, covering the extensive internal aspect of the jaw, is fused to the dentary along both the dorsal and ventral spleniodentary sutures, but the remnant suture lines are still recognizable. The anterior end of the splenial is strongly notched, and a short anterior opening for the Meckelian canal is developed under the first three dentary teeth. Anteriorly, the ventral spleniodentary suture is medial in position, but posterior to the midpoint of the tooth row it is ventrally and then laterally located; hence, the posterior half of the ventral suture is not shown in medial view. The splenial has a depression at its central part where two (contra Estes, 1964:fig. 54) Meckelian foramina (anterior inferior alveolar foramen and anterior mylohyoid foramen) open; these are the passageways for fibers of cranial nerve V_3. The anterior inferior alveolar foramen is smaller and more ventrally located than the anterior mylohyoid foramen (UALVP 33921, a left mandible from the Scollard Formation also shows the same feature, see Fig. 18B). The external surface of the dentary is slightly convex; it is mostly smooth, but the ventral edge is slightly scarred, reflecting the attachment of hyoid musculature. The six external inferior alveolar foramina shown on the specimen are small, rounded, increase slightly in size posteriorly, and are unequally spaced from each other. The posteriormost foramen is probably located under the 12th tooth position, where the specimen is broken.

The dentary has 13 teeth preserved, but they are all partially dissolved, showing no pattern of cusps. The total tooth count for this specimen is estimated as no more than 16, as only about four positions can be added posterior to the anterior inferior alveolar foramen (see Estes, 1964). The tooth row is straight in dorsal view, lacking the curvature seen in *Leptochamops* and *Meniscognathus.* The sulcus dentalis is lost entirely, and the remnant lateral parapet is so low (less than one-third of the tooth height) that the term "subpleurondont" is incongruous for this condition; we believe that the term "subacrodont" (sensu Estes, 1964) is more appropriate.

Two other referred specimens (UALVP 29771, 29780), both from the Wounded Knee locality of the Frenchman Formation, probably pertain to *H. placodon*; they are mandible fragments bearing water-worn teeth (Fig. 18C, D). Both of the specimens show spleniodentary fusion, with more extensive fusion seen on UALVP 29771, in which the suture is barely recognizable.

Discussion.—Haptosphenus placodon was originally named and described by Estes (1964) on the basis of several dentary specimens from the Lance Formation, Wyoming. This species was later reported from the Hell Creek Formation (Estes et al., 1969; Bryant, 1985), Montana, and now from the Scollard and Frenchman formations, Alberta and Saskatchewan. The newly discovered specimen SMNH P1920.23 resembles the holotype (UCMP 46035) in general jaw configuration, in having a subacrodont dentition and extensive spleniodentary fusion; therefore, it is clearly referrable to the same species. One difference between the two specimens seems to be that the holotype shows one foramen penetrating the splenial for cranial nerve V_3, while SMNH P1920.23 has two; however, the holotype is broken at the location of the anterior mylohyoid fo-

ramen, and the breakage may have caused the "absence" of this foramen on the specimen. Accordingly, the Frenchman specimen, with two internal Meckelian foramina, represents the natural condition of the jaw of this lizard.

Estes (1964) referred *Haptosphenus placodon* to the family Teiidae, and hinted at a tupinambine relationship by stating that "the closest resemblances of *Haptosphenus* seem to be with *Chamops,* differing from the latter both in bone fusion and in having almost acrodont teeth; it may be an aberrant teiid derived from a *Chamops*-like ancestor" (Estes et al., 1969:19). But more recently, Estes (1983*a*) referred *Haptosphenus* to the extinct Polyglyphanodontinae, while noticing that "it is possible that when skull material is known that it will prove referable to an extinct family" (Estes, 1983*a*:83). It is difficult to clarify further the phylogenetic relationships of this lizard until more complete materials are found.

The Lancian *Haptosphenus* is indeed highly specialized, with extensive fusion of the mandibular elements and a subacrodont dentition (Estes, 1964, 1983*a*; Estes et al., 1969), and its relationship with modern teiids is much less clear than that of other teiids from the same horizon (Estes and Báez, 1985). The fusion of some mandibular elements occurs independently in several modern lizard families (e.g., Iguanidae*, Gekkonidae, Xantusiidae) that are obviously remote from *Haptosphenus*. This feature has not been reported in any modern teiids (see later discussion) to which *Haptosphenus* is possibly related; however, some Cretaceous teiids show the potential development of this feature: in some individuals of *Sphenosiagon,* the large splenial is firmly articulated with the dentary, although the mandible is lightly built; and in *Gerontoseps,* the splenial can be partially fused to the dentary along the dorsal spleniodentary suture (see Gao and Fox, 1991, and relevant discussion in this paper). In spite of these similarities, the relationships of *Haptosphenus* with the above-mentioned two teiids are still obscure, as the phylogenetic value of these characters is still poorly understood.

Another unusual character of this lizard, the subacrodont dentition, is associated with the loss of the sulcus dentalis and a great reduction of the lateral parapet of the dentary. Among squamates, including amphisbaenians, the true acrodont condition is independently evolved in acrodontan iguanians, and trogonophid and oligodontosaurid amphisbaenians (Zangerl, 1944; Gans, 1958, 1978; Estes, 1975). It seems clear that acrodonty in the Acrodonta Cope, 1864 (= Chamaeleonoidea Moody, 1980; Chamaeleonidae sensu Frost and Etheridge, 1989) is unlikely to be associated with the subacrodonty of certain teiids, such as *Haptosphenus,* as the relationships of the two groups are remote, as reflected in their classification in two different infraorders.

Comparing the subacrodonty of *Haptosphenus* with the acrodonty of amphisbaenians raises another problem. A sister-group relationship of amphisbaenians with Teiidae (sensu lato; = Teiioidea Estes et al., 1988) has been suggested by Boulenger (1884), Bogert (1964), and Böhme (1981), and supported by several other authors (Saint-Girons, 1968; Lécuru, 1969; Presch, 1975; Schwenk, 1988). However, the subacrodont condition in *Haptosphenus* is evidently nonhomologous to the acrodonty in those oligodontosaurid and trogonophid amphisbaenians, because the more primitive pleurodont condition occurs in both Teiioidea and Amphisbaenia (see Estes, 1983*a*), and the monophyly of each of the two groups is well supported by a suite of synapomorphies (Estes et al., 1988).

Based on the available evidence from jaw shape and tooth form, it seems more reasonable to accept Estes' (1964, 1983*a,* 1985) assignment of *Haptosphenus* as a member of Teiidae than of any other lizard family. In particular, Estes (1983*a,* 1985) suggested a possible relationship of this lizard to the Polyglyphanodontinae (sensu Estes, 1983*a*), which includes two genera (*Polyglyphanodon* Gilmore, 1940 and *Adamisaurus* Sulimski, 1972) also having a subacrodont dentition. *Polyglyphanodon* is known from the Lancian North Horn Formation, Utah (Gilmore, 1940, 1942*b,* 1943*b*), and *Adamisaurus* is from the mid-Campanian Djadochta Formation of the Gobi Desert (Sulimski, 1972, 1978). The latter two lizards have greatly expanded crushing teeth, while those in *Haptosphenus* are tricuspid. In addition, the teeth of *Adamisaurus* have well-developed resorption pits, while the subacrodont teeth of *Haptosphenus* are apparently not replaced. These differences throw doubt on the inclusion of *Haptosphenus* in the Polyglyphanodontinae. Here, we draw attention to the close resemblance of this aberrant form to the extant *Draceana,* as these two lizards show the following similarities: 1) dentary short, robust, and strongly tapering upward anteriorly; 2) splenial extends posteriorly to the lateral surface of the jaw; 3) location and number of internal mandibular foramina comparable; 4) mandibular elements fused or tend to be fused; 5) subacrodont tooth attachment. If these similarities are phy-

logenetically significant, *Haptosphenus* may be a member of the Teiinae (sensu Estes, 1983*a*).

Genus *Stypodontosaurus,* **new genus**

Etymology.—stypos + *odontos* + *sauros* (Greek, masculine), meaning "stumpy-toothed lizard," in reference to the short and stout teeth of this lizard.

Type Species.—Stypodontosaurus melletes, new species.

Range.—Upper Cretaceous, North America.

Diagnosis.—As for the type and only known species.

Stypodontosaurus melletes, **new species**
(Fig. 19)

Etymology.—melletes (Greek, masculine), meaning "delayer," in reference to its late geologic occurrence in the Late Cretaceous, and its delayed recovery in 1991 from the screen-washed concentrate collected in the 1960s.

Holotype.—UALVP 29844, a nearly complete right dentary having 16 teeth and the base of another.

Type Locality and Horizon.—KUA-1 locality (Lillegraven, 1969), Red Deer River valley near the village of Scollard, central Alberta; Upper Cretaceous Scollard Formation (Lancian).

Known Distribution.—Known only from the type locality and horizon.

Diagnosis.—Relatively large Late Cretaceous teiid; dentary greatly elongate and robust, very shallow anteriorly, with no ventral buttress developed; subdental shelf deep and strong, maximum depth about equal to tooth height; sulcus dentalis narrow and deep; dentary teeth short, stumpy, and well separated from each other; tooth bases circular to slightly compressed laterally in cross section; tooth crowns unicuspid, but with well-defined crest encircling horseshoe-shaped depression lingually; apical cusp small, and cuspation not changing significantly along tooth row; tooth attachment subpleurodont, with over half of tooth height projecting above lateral parapet; basal cementum little developed lingually.

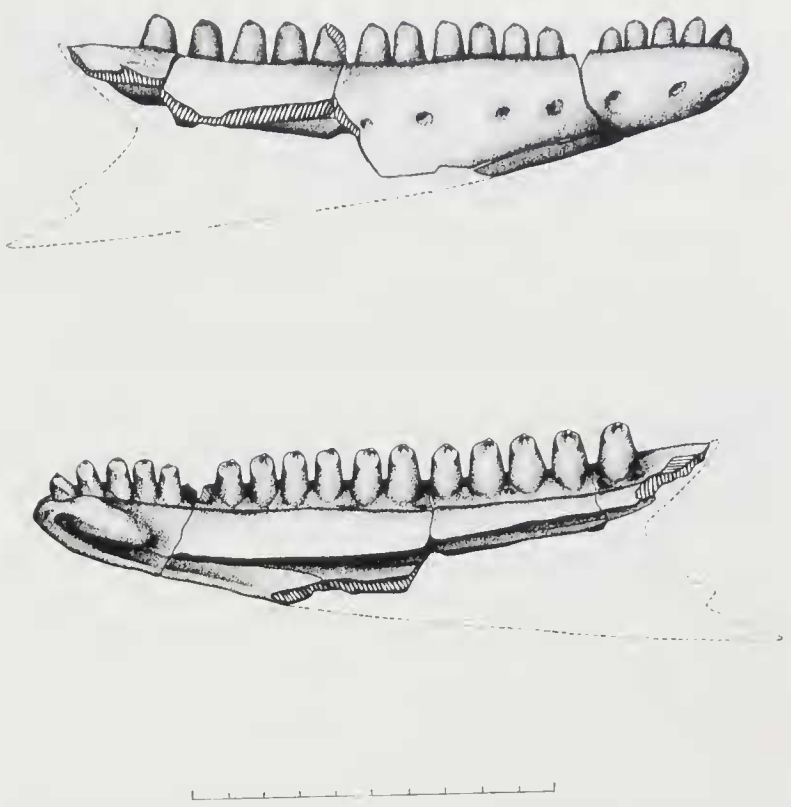

Fig. 19.—*Stypodontosaurus melletes,* new genus and species, Scollard Formation, Alberta: UALVP 29844 (holotype), incomplete right dentary, lateral (above) and medial (below) views. Scale = 10 mm.

Description.—The holotype and only known specimen (UALVP 29844, Fig. 19) is a well-preserved right dentary, lacking only its posteroventral part. The dentary is basically straight in dorsal view, but is curved anteriorly at the mandibular symphysis. The shape of the dentary indicates that the mandible of this lizard is shallow, elongated, but robustly built. Medially, the dentary bears a sturdy subdental shelf, which is greatly deepened over the anterior two-thirds of the specimen, but abruptly reduced over the posterior one-third. The maximum depth of the shelf is about the same as the tooth height. The anterior end of the shelf bears a robust medial process, which forms the main part of the strong mandibular symphysis, although the anterior tip of the jaw is very shallow. The ventral surface of the shelf bears a well-developed groove for the spleniodentary articulation. The groove shows that the splenial (missing on the specimen) extended well anteriorly, to beneath the sixth tooth position. The dorsal edge of the subdental shelf, which is straight in medial view, is developed as a sharp and strong ridge along the medial border of the narrow, deep sulcus dentalis. The Meckelian canal is strongly restricted under the first five tooth positions, where the fissure-like anterior opening of the canal is located, but abruptly increases in depth and width posteriorly from the sixth tooth.

The dentary teeth are short, stout, pillar-like, and widely spaced from each other. With a faint central cusp that is slightly tipped medially, the tooth crowns can be technically termed unicuspid, but characteristically have well-defined side ridges (crests) running laterally from the cusp, then down and medially, enclosing a more or less horseshoe-shaped medial surface of the crown. The tooth attachment is subpleurodont, with the lateral parapet of the dentary remaining less than half of the tooth height. The basal deposit of cementum is extensive as in other teiids, but appears to be absent lingually. The size of the dentary and the absence of replacement pits indicate that the holotype represents a mature individual in which tooth replacement has been suppressed. The dentary has 17 teeth (16 complete teeth and the base of another) for the complete tooth row of the holotype. A dorsal view of the specimen shows that the tooth row is straight for the 12 posterior teeth, but slightly curved towards the symphysis for the first five teeth.

The lateral surface of the dentary is slightly convex for the anterior two-thirds of the bone, but the posterolateral part bulges strongly as shown on the specimen, a result of the posterior widening of the Meckelian canal. The posteroventral part of the den-

tary is missing, but the remainder shows that the ventral border turns strongly towards the medial side of the jaw; accordingly, the ventral spleniodentary suture faces ventromedially. The lateral surface has seven inferior alveolar foramina, which are small, rounded, and more or less evenly spaced in a horizontal row.

Discussion.—Collected from the Scollard Formation, UALVP 29844 is the holotype and the only known specimen of this new genus and species. The specimen shows a conspicuous deposit of cementum around the tooth bases except lingually, and a large splenial indicated by the widely open Meckelian canal (see Estes et al., 1988, for evaluation of these character states). On the basis of these features, *Stypodontosaurus* can be referred to the Teiidae. Other character states, such as a well-developed sulcus dentalis, a subpleurodont dentition, and suppression of tooth replacement, are also indicative of its affinity with the family Teiidae. However, this referral is tentative, as the crowns of the dentary teeth are in some degree similar to those of the African *Cordylus breyeri* (Cordylidae), and the depth and robustness of the subdental shelf also recall the cordylids. Therefore, it is possible, when more and better preserved specimens are recovered, that *Stypodontosaurus* may be assigned to another family.

Compared with other fossil and extant teiids, the most conspicuous features of this new lizard are the extremely deep subdental shelf, and the short, stout teeth with a unique crown pattern as described above. A strong subdental shelf makes the jaw more solidly built, and hence strengthens the biting mechanism. This type of crushing jaw mechanism is often associated with low-crowned, stout teeth in other teiids, such as *Chamops, Tupinambis,* and *Dracaena.* The tooth crowns of *Stypodontosaurus* are laterally compressed, having a faint central cusp that tips medially, and lateral ridges that curve down and medially. This pattern is clearly different from those of Judithian teiids, such as *Gerontoseps,* in which a narrow crown bears a rounded cusp with weakly developed lateral ridges. It is difficult, at this stage, to determine whether this crown pattern is derived from a tricuspid condition in which ridges linked the side cusps with the main cusp, or is a more primitive condition in which there were no side cusps originally. The dentary teeth show no replacement pits at the tooth bases, perhaps as a consequence of age, in which tooth replacement was suppressed.

In general, the referral of *Stypodontosaurus* to the Teiidae is tentative. The jaw configuration and the tooth form of this new lizard are so different compared to other known teiids, that we find no evidence on which to make a reasonable interpretation about its relationships below the familial level. However, it is possible to include this form in the problematic subfamily Polyglyphanodontinae, which includes several Late Cretaceous teiids having aberrant tooth forms.

Family Scincidae Gray, 1825

The family Scincidae is probably the most successful modern lizard family, as evidenced by its large numbers of species and individuals, as well as its worldwide distribution. The family is estimated as having 600–1275 living species (probably around 1000; Mattison, 1989), and is widespread not only in Australia, Southeast Asia, and Africa, but also in Europe and the Western Hemisphere. The Scincidae are usually subdivided into four subfamilies (Greer, 1970; Estes, 1983*a*): Feyliniinae Camp, 1923 and Acontiinae Gray, 1845, both of which are presently restricted to Africa; Scincinae Gray, 1925, which are presently Old World exclusive of Australia in distribution; and Lygosominae Mittelman, 1952, which are worldwide and are the only subfamily occurring in both Australia and South America (data from Greer, 1970; Estes, 1983*a*; Mattison, 1989).

Despite their great diversity and wide geographical distribution today, the Scincidae have a poor fossil record (Estes, 1983*a,* 1983*b*). There is no pre-Miocene record from Asia, Africa, or Australia, where extant scincids are widespread; and as discussed later in this paper, several supposed early scincids may have relationships with other groups rather than the Scincidae: Late Cretaceous *Contogenys* Estes, 1969*b* may be more closely related to Xantusiidae than to the Scincidae; *Sauriscus* Estes, 1964 may have a cordylid affinity (Estes, 1983*a,* 1983*b*), and Upper Jurassic *Mimobecklesisaurus* Li, 1985 should be relocated to the Paramacellodidae. However, Rowe et al. (1992) have recently described a scincid with a durophagous dentition from the late Campanian (Judithian) of Texas, accompanied there by a second, *Sauriscus*-like skink. The oldest record for the Scincidae is provided by recently described incomplete jaws with teeth from the Lower Cretaceous of Spain (Richter, 1994).

Genus *Penemabuya,* **new genus**

Etymology.—pene (Latin), meaning "near, almost"; *mabuya* (Latin), a kind of skink.

Type Species.—Penemabuya antecessor, new species.

Range.—Upper Cretaceous, North America.

Diagnosis.—As for the type and only known species.

Penemabuya antecessor, new species
(Fig. 20, 21A–C)

Etymology.—antecessor (Latin), meaning "forerunner," in reference to the *Mabuya*-like dentary morphology of this ancient skink.

Holotype.—UALVP 29789, incomplete right dentary having six teeth and the broken bases, as well as vacant spaces, of 16 others.

Type Locality and Horizon.—MR-6 locality, Verdigris Coulee, approximately 30 km east of the village of Milk River, southern Alberta; upper member of the Milk River Formation (Aquilan), Upper Cretaceous.

Referred Specimens.—UALVP 29788, 29827–29828, and several unnumbered jaw fragments; all topotypic specimens.

Known Distribution.—Upper Cretaceous Milk River Formation (Aquilan), southern Alberta.

Diagnosis.—A small Late Cretaceous scincid resembling in dentary structure and dentition primitive extant scincids, such as *Mabuya*; dentary shallow, slender, and elongate; subdental shelf narrow, extending ventrally nearly to level of ventralmost margin of dentary external to Meckelian canal; sulcus dentalis poorly developed; Meckelian canal narrow, anterior part opening ventrally; dentary teeth tall, slender, somewhat recurved, especially posteriorly along tooth row; tooth crowns unicuspid, with weak anterior and posterior crest, and faint medial striations; tooth attachment pleurodont, with one-half to three-quarters of tooth height attached to lateral parapet, depending on position in tooth row.

Description.—Two specimens of this new skink, UALVP 29789 (the holotype) and UALVP 29788, are well preserved. The holotype (Fig. 20, 21A, B) is a nearly complete right dentary, with only the very posterior end missing. It is shallow, slender, and greatly elongated. The lateral surface of the dentary is smooth, showing no sculpture. Five inferior alveolar foramina are unequally spaced from one another, and each shows a certain degree of anterior elongation. Below the foramina, the ventral edge of the dentary turns sharply medially, tending to enclose the Meckelian canal, and forming a more or less flat surface for the anterior two-thirds of the dentary ventral border. Medially, the specimen bears a slender but prominent subdental shelf, which gently curves upward and is diminished posteriorly. The anterior tip of the shelf turns dorsomedially, forming most of the delicate mandibular symphysis. Below the shelf, the Meckelian canal is extremely narrow along its anterior half but slightly increases in depth posteriorly. Judging from the articulation surface, the missing splenial seems to have been a shallow and slender bone that ventromedially covered the posterior two-thirds of the Meckelian canal, leaving the anterior third open ventrally. Posteriorly within the Meckelian canal, the posterior interior alveolar foramen opens below the 20th tooth position, and no intramandibular septum is developed in the canal.

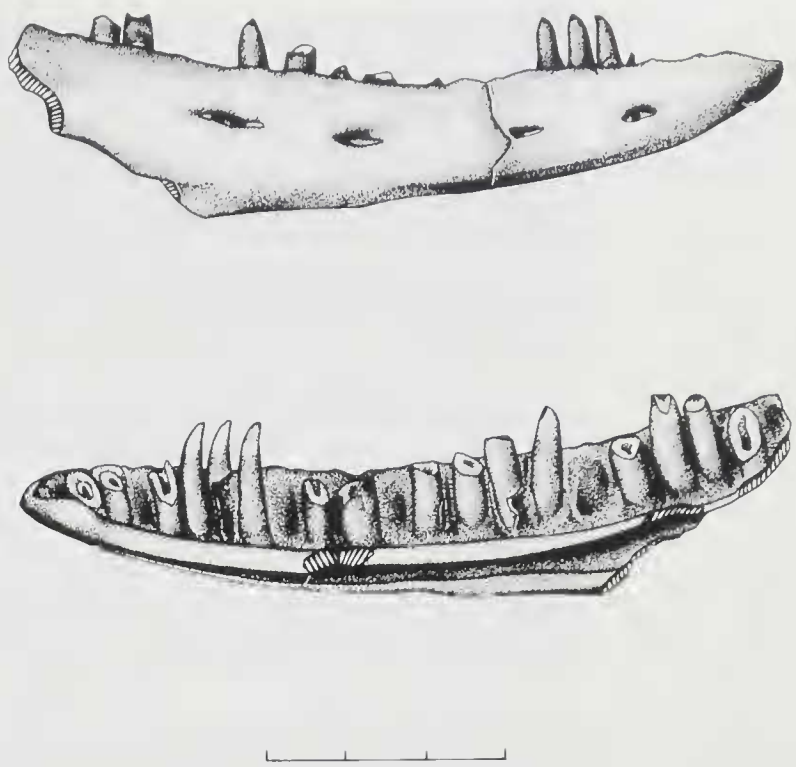

Fig. 20.—*Penemabuya antecessor,* new genus and species, Milk River Formation, Alberta: UALVP 29789 (holotype), incomplete right dentary, lateral (above) and medial (below) views. Scale = 3 mm.

The dentary teeth are pleurodont, with about two-thirds of the tooth height attached to the well-developed lateral parapet of the jaw. There are 22 tooth positions on the preserved part of the holotype; possibly only the two posteriormost teeth are missing (judging from the posterior extremity of the subdental shelf that corresponds to the termination of the tooth row). Four teeth (seventh through the ninth, and the 17th) are completely preserved, and two others (the 20th and 21st) are nearly complete with just the tips broken; the rest of the tooth row consists of either broken bases or teeth that are missing entirely. The tooth shafts are slender and the crowns are unicuspid and pointed, with weak medial striations. There is no notable change of tooth structure along the tooth row, except that the anterior teeth have slightly recurved crowns. The basal part of the eighth tooth has been largely resorbed, but its upper half is still functional and weakly attached to the parapet.

Another well-preserved specimen, UALVP 29788 (Fig. 21C), is also a right dentary but shows all of the positions in the tooth row. On this specimen, seven teeth are complete; the other 17 are tooth spaces or broken bases, making the full tooth count 24 for this dentary. The specimen shows close resemblances to the holotype in shape and structure of dentary, and in crown pattern of the teeth. However, UALVP 29788 has cementum around the tooth bases, and shows an unusual pattern of tooth replacement that is different from that in the holotype. In this specimen, the sixth and the seventh teeth from the back are new replacement teeth that have developed posteromedially to the replaced teeth and have already reached the functional height of the tooth row, but the old teeth (being replaced) are not excavated and are still

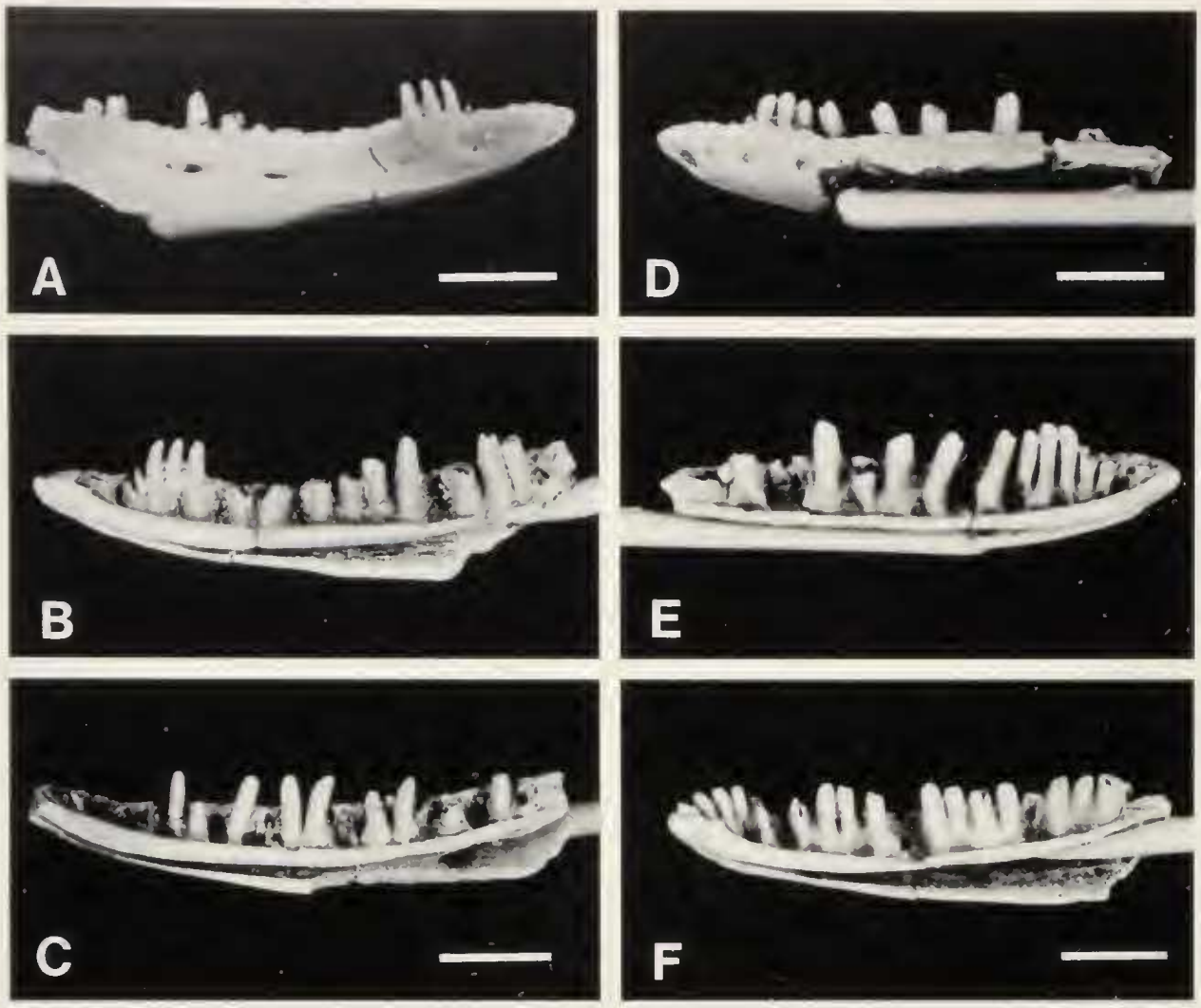

Fig. 21.—*Penemabuya antecessor,* new genus and species, Milk River Formation, Alberta: A, B, UALVP 29789 (holotype), incomplete right dentary, lateral and medial views; C, UALVP 29788, right dentary, medial view. *Orthrioscincus mixtus,* new genus and species, Oldman Formation, Alberta: D, E, UALVP 29747 (holotype), incomplete left dentary, lateral and medial views; F, UALVP 29904, right dentary, medial view. Scale = 2 mm.

functional together with the new teeth. This type of tooth replacement is not only different from the "iguanid method" in scincids (Edmund, 1969) but also the "varanid method" in most anguimorphans (Edmund, 1969), and apparently represents an abnormal condition.

Discussion.—Osteologically, the family Scincidae is characterized by several synapomorphies, including a jugal–squamosal contact, a closure of the supratemporal fenestra, and a medial extension of the palatines to form a bony secondary palate (see Estes et al., 1988). Although these characters are unavailable for the screen-washed materials in this study, a combination of the following character states on the jaws of *Penemabuya* is strongly indicative of its affiliation with primitive scincids: a slender, shallow, strongly elongated dentary; a narrow Meckelian canal, which tends towards complete closure anteriorly; a *Mabuya*-like pleurodont dentition in which the shafts are slender and the crowns unicuspid and pointed, bearing medial striae; and a posterolingual (intermediate) replacement pattern.

Among modern scincids, *Mabuya* Fitzinger, 1826 and *Eumeces* Wiegmann, 1834 (Estes, 1983*a*: the most primitive living skink) are the two most widespread genera geographically (Greer, 1970; Peters et al., 1986; Mattison, 1989). Besides the character states discussed by Greer (1970), we here draw attention to differences between the two genera in jaw structure and tooth form. These differences are: 1) the dentary of *Mabuya* is generally much more slender and elongated than that of *Eumeces*; 2) the spenial is much more reduced in the former, and does not extend anteriorly beyond the midpoint of the tooth row; 3) the Meckelian canal of *Mabuya* is often closed anteriorly by fusion of the dentary, but is commonly open in *Eumeces*; 4) the marginal teeth of *Mabuya* are cylindrical and pointed, while in *Eumeces,* the tooth shafts are more or less anteroposteriorly compressed, and the crowns are wider and have lateral crests with strong medial striations; 5) tooth replacement is more frequent in *Mabuya* than in *Eumeces*; correspondingly, the former has a basal foramen at each tooth base, while the latter does not.

A comparison of the new skink from the Milk

River Formation with available specimens of extant skinks indicates that the new species is probably more closely related to *Mabuya* than to *Eumeces*: it shares with *Mabuya* character states such as having a slender and elongate dentary, a greatly reduced splenial (indicated by a narrow Meckelian canal), and slenderly cylindrical and pointed teeth. As briefly discussed above, these are probably derived character states in the Scincidae. In addition, *Penemabuya* clearly shows a tendency towards closure of the Meckelian canal by medial extension of the ventrolateral edge of the dentary.

The biogeographical origin of the New World skinks (in particular, the *Mabuya* group) is an open question, although Dunn (1936) noted the close relationship of the New World species with the African species of the genus; Darlington (1957:194) believed that the New World *Mabuya* "may have come from Africa on drift"; and Greer (1970:180) noted the difficulty of determining "whether the group arrived from Asia via the Bering Land Bridge or from Africa by over-water rafting," but favored the latter possibility. Greer (1970:180) also stated that "the lack of diversity of the New World species may indicate that the group has not been in the New World very long."

Discovery of the new skink from the Upper Cretaceous Milk River Formation indicates that the *Mabuya*-like scincids have inhabited the North American continent since early Campanian time (some 83 Myr ago, Harland et al., 1990), and with the somewhat younger occurrences cited by Rowe et al. (1992), along with the species described below, may count in support of a possible northern continental origin for the New World skinks. Further, the Campanian radiation of North American scincids implies a prior history on the continent of some unknown length, one that is in agreement with European evidence of the establishment of the Scincidae in the eastern parts of the Euramerican continent by at least the Early Cretaceous (Richter, 1994).

Genus *Orthrioscincus*, **new genus**

Etymology.—*Orthrios* + *skinkos* (Greek, masculine), meaning "early skink."

Type Species.—*Orthrioscincus mixtus*, new species.

Range.—Upper Cretaceous, North America.

Diagnosis.—As for the type and only known species.

Orthrioscincus mixtus, **new species**
(Fig. 21D–F, 22)

Etymology.—*Mixtus* (Latin), referring to the combination of *Eumeces*-like characters of the dentary and *Gerrhosaurus*-like teeth of this lizard.

Holotype.—UALVP 29747, incomplete left dentary having seven teeth and tooth bases as well as spaces for ten others.

Type Locality and Horizon.—Outcrop of the Oldman Formation near Irvine, in Sec. 31, Tp. 11, R 2, W 4, about 40 km east of Medicine Hat, southeastern Alberta; Upper Cretaceous Oldman Formation (Judithian).

Referred Specimen.—UALVP 29904, topotypic, nearly complete right dentary bearing 19 tooth positions.

Known Distribution.—Upper Cretaceous Oldman Formation (Judithian), southeastern Alberta.

Diagnosis.—A small Late Cretaceous scincoid having a dentary structure broadly resembling those of primitive extant *Eumeces*-like skinks, but with tooth morphology more similar to that of cordylid gerrhosaurs. Dentary slender, elongate, and delicately built; differing from *Penemabuya* in having a deeper dentary anteriorly, slightly narrower subdental shelf, and weaker sulcus dentalis; dentary teeth strongly bicuspid, with somewhat rounded main cusp and prominent anterior cusp, set off from main cusp by lingual and more prominent labial groove; enamel of main cusp with striae lingually and faint striae labially; tooth attachment pleurodont, with approximately two-thirds of tooth height attached to lateral parapet. Differing from *Gerrhosaurus* Wiegmann, 1828, in having much more slender and curved subdental shelf, anterior cusp less clearly separated from the posterior main cusp, and main cusp not recurved.

Description.—The holotype UALVP 29747 (Fig. 21D, E; 22) is a tooth-bearing left dentary, which has only the posteroventral part missing. The specimen is designated as the holotype because it clearly shows the tooth form of this new species, while the referred specimen, UALVP 29904 (Fig. 21F), a right dentary, has less well-preserved teeth but shows the nearly complete configuration of the dentary.

The holotype dentary is shallow, straight, elongated, and lightly built, as in most extant scincoids. The lateral surface is incomplete, but was apparently smoothly convex like that in UALVP 29904. Four small inferior alveolar foramina clearly shown on the specimen are unevenly spaced from one another in a horizontal row. Another (probably the seventh) foramen is recognizable by its dorsal border at the broken edge of the jaw and is located lateral to the 13th tooth position, close to the posterior interior alveolar foramen within the Meckelian canal. Medially, the dentary bears a slender subdental shelf, the maximum depth of which is much less than one-third of the tooth height, and the

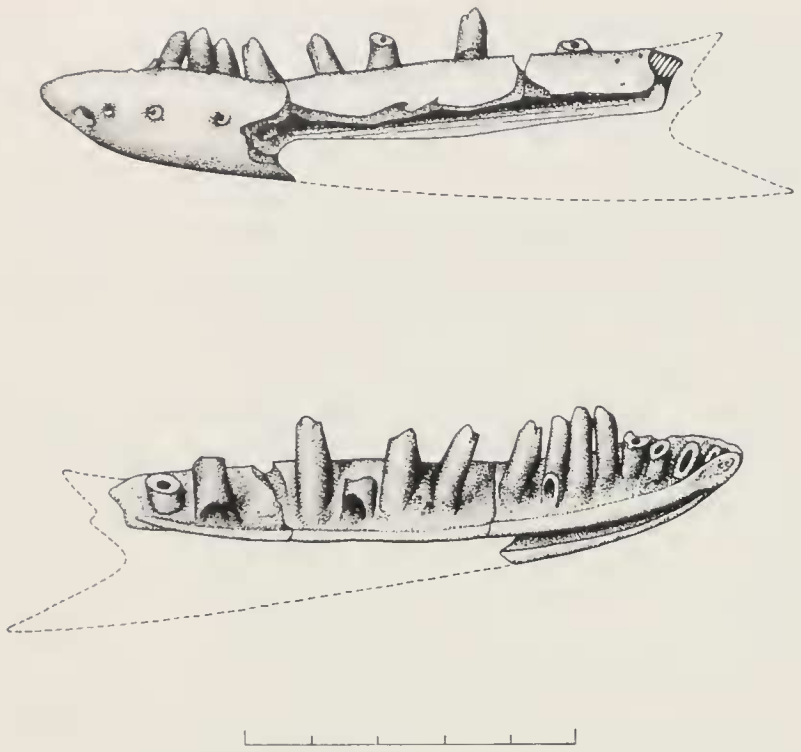

Fig. 22.—*Orthrioscincus mixtus,* new genus and species, Oldman Formation, Alberta: UALVP 29747 (holotype), incomplete left dentary, lateral (above) and medial (below) views. Scale = 5 mm.

shelf strongly curves dorsally at its anterior end. These proportions closely resemble those of the extant scincid *Eumeces* in comparable parts. Above the subdental shelf and medial to the tooth row is a weakly developed sulcus dentalis, which forms a shallow trough. Below the shelf, the Meckelian canal posteriorly has a maximum depth about equal to the tooth height, but the canal becomes increasingly narrow and faces ventromedially towards the anterior end of the jaw. The posterior interior alveolar foramen opens into the Meckelian canal under the 14th tooth position (between the 13th and the 14th on the holotype).

Both the holotype and UALVP 29904 document the complete dentary tooth row; the two specimens together indicate that the dentary tooth count of this lizard is variable, ranging at least between 17 (on the holotype) and 19 (on UALVP 29904). The tooth form is clearly shown on the holotype, while the crowns of the UALVP 29904 are partially dissolved, showing no detail about the cusp pattern. The dentary teeth are pleurodont, with about one-third of the tooth height projecting above the lateral parapet of the dentary. Several broken tooth shafts show that the anterior and the middle teeth are slightly compressed anteroposteriorly, but the posterior ones (the last four or five) are cylindrical. In general, the teeth are close to one another along the tooth row, but the spacing is variable as the result of tooth replacement. The first five or six teeth are slightly procumbent, conical, and slightly shorter than those midway along the tooth row. The posterior teeth are slightly stronger than the middle teeth. The crowns of the middle and posterior teeth are bicuspid, having a small, pointed, low anterior cusp, and a high and blunt posterior main cusp, which is weakly striated on its medial surface. This particular cusp pattern in a certain degree resembles that of the extant *Gerrhosaurus* (Cordylidae), but conspicuous differences in jaw structure including the robustness of the subdental shelf imply that this similarity may be convergent.

Both the holotype and UALVP 29904 show that several teeth have developed an excavation posteromedially at the tooth bases. This indicates an intermediate replacement pattern (Edmund, 1969), which differs from the "iguanid pattern" in having the replacement tooth developed posteromedial to (rather than directly within) the old tooth, and from the "varanid pattern" in having a resorption cavity, although this is shallow. On the holotype, the ninth tooth is loosely attached to the dentary, with the tooth base being slightly off the main line of the tooth row. Behind this tooth is a large space for the tenth tooth, which has already fallen from the tooth row. This abnormal condition of the ninth tooth is possibly the result of mechanical damage, because this tooth is large enough to have been fully functional, but would have been attached to the lateral parapet in the normal condition.

UALVP 29904 is a nearly complete right dentary from the type locality. This specimen resembles the holotype in overall size and shape, number and spacing of external foramina, length of tooth row, development of subdental shelf and sulcus dentalis, and configuration of the Meckelian canal. This specimen is referred to the same species as the holotype based on these resemblances; however, all of the teeth (19 in total) have the crowns partially dissolved, and the poor preservation of the crowns makes this referral somewhat uncertain.

Discussion.—The new lizard *Orthrioscincus* shows a combination of a primitive scincid configuration of the dentary with a *Gerrhosaurus*-like tooth form (e.g., compare UA 382, *Gerrhosaurus flavigularis* with UALVP unnumbered specimen of *Eumeces inexpectatus*). This mosaic of characters makes the referral of this form at a familial level uncertain, since the Scincidae and Cordylidae are primarily distinguished from each other by skull and external structures (see Estes et al., 1988) that are not preserved in the Oldman specimens. However, this lizard could be referred to the Scincidae based on its *Eumeces*-like shape of dentary, with its tooth form convergent on that of *Gerrhosaurus.*

Discovery in the Oldman Formation of *Orthrioscincus* with a *Gerrhosaurus*-like dentition reveals the following possibilities: 1) ancestral gerrhosaurines once had a much wider geographical distribution than they have today. *Orthrioscincus* may represent one of the primitive members of the group that occupied similar ecological niches in North America as does *Gerrhosaurus* in Africa and Madagascar today. Indeed, with reference to tooth form only, we would place *Orthrioscincus* in the Cordylidae rather than Scincidae. However, the jaw configuration of this new form strongly indicates it is a primitive skink. From current understanding of scincoid evolution, the slenderness and the dorsal curvature of the subdental shelf anteriorly are likely more-derived character states than the stronger and straight subdental shelf in extant gerrhosaurine cordylids. Accordingly, if *Orthrioscincus* is regarded as a primitive gerrhosaur, it would be difficult to explain why such an early member of the group (Judithian in age) has such a derived morphology

in the dentary. 2) *Orthrioscincus* may be a primitive member of the Scincidae. In this interpretation, the similar jaw configuration, especially its slenderness and the curvature of the subdental shelf, is the guide to relationship; in that case, the similarity in cusp pattern to *Gerrhosaurus* indicates a similar type of food preference. According to Mattison (1989:164), extant *Gerrhosaurus* lizards "eat a substantial amount of plant material, but are otherwise insectivorous."

Nevertheless, *Orthrioscincus* is a Judithian member of the Scincoidea, as it possesses the combination of a primitive scincid, *Eumeces*-like dentary structure and *Gerrhosaurus*-like dentition. Here we tentatively place this genus in the Scincidae, regarding the similarity in dentary structure as a reliable indication of relationship, and the *Gerrhosaurus*-like crown pattern as convergent.

Genus *Aocnodromeus,* **new genus**

Etymology.—Aoknos + *dromeus* (Greek, masculine), meaning "restless runner."

Type Species.—Aocnodromeus corrugatus, new species.

Range.—Upper Cretaceous, North America.

Diagnosis.—As for the type and only known species.

Aocnodromeus corrugatus, **new species** (Fig. 23, 24A–D)

Etymology.—Corrugatus (Latin), meaning "wrinkled," in reference to the wrinkled enamel on the tooth crown of this lizard.

Holotype.—UALVP 29905, a nearly complete left dentary bearing 11 teeth and spaces for five others.

Type Locality and Horizon.—MR-6 locality, Verdigris Coulee, approximately 30 km east of the village of Milk River, southern Alberta; upper member of the Milk River Formation (Aquilan), Upper Cretaceous.

Referred Specimen.—UALVP 29906, topotypic left dentary fragment with nine anterior tooth positions.

Known Distribution.—Currently known only from the type locality and horizon.

Diagnosis.—A Late Cretaceous scincid distinguished from all other species by its possession of the following combination of character states: dentary robustly built, having strong subdental shelf and well-defined sulcus dentalis; Meckelian canal shallow, narrow, and opening ventrally anteriorly; dentary teeth solidly subcolumnar, widely spaced; tooth attachment pleurodont, with lateral parapet high, about two-thirds of tooth height; tooth crowns broad, unicuspid, with cusp apex posterior to midpoint of crown, medially concave and striated; posterior teeth molariform, with laterally compressed and squared-off crowns.

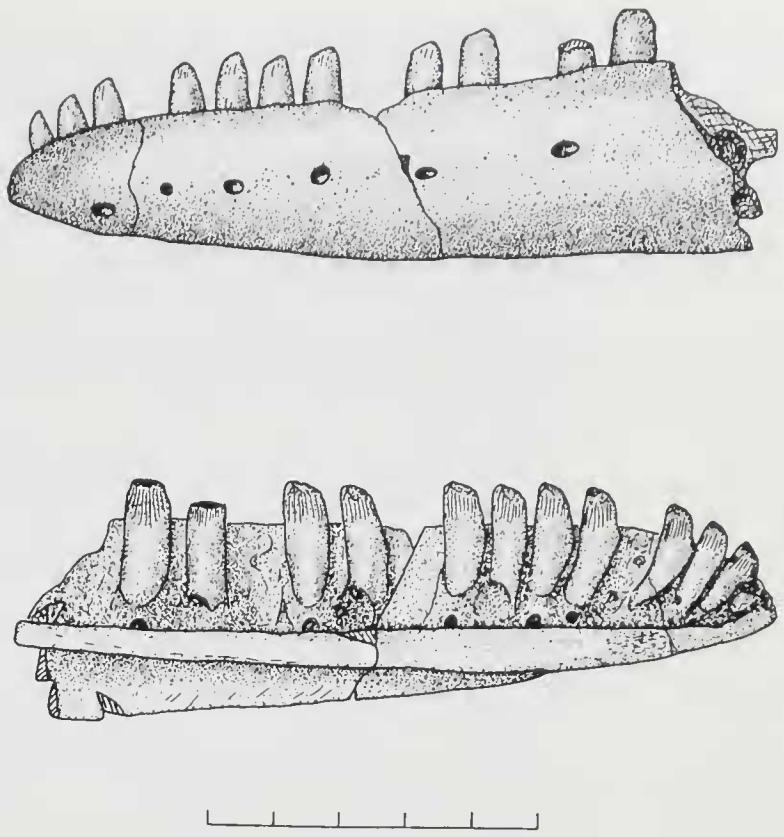

Fig. 23.—*Aocnodromeus corrugatus,* new genus and species, Milk River Formation, Alberta: UALVP 29905 (holotype), nearly complete left dentary, lateral (above) and medial (below) views. Scale = 5 mm.

Description.—The holotype UALVP 29905 (Fig. 23; 24A, B) is well preserved, showing most of the dentary and 16 tooth positions. The dentary is broken posteriorly at the 16th tooth position, but with no evidence of the posterior interior alveolar foramen that normally opens close to the posterior end of the dentary tooth row. The proportions of the dentary indicate that the jaw was shallow, elongated, but quite robustly built. The lateral surface of the dentary is smooth, and gently convex both dorsoventrally and anteroposteriorly. This surface has six small and round inferior alveolar foramina that are widely spaced, with the space between them increasing gradually posteriorly. The last foramen on the specimen is located lateral to the 14th tooth position.

In medial view, the dentary shows a straight and robust subdental shelf, which gently decreases its depth posteriorly. The maximum depth of the shelf is slightly less than half of the tooth height, and the anterior end of the shelf forms a relatively strong mandibular symphysis. Dorsally on the shelf is a well-defined sulcus dentalis medial to the tooth row, but the sulcus lacks a sharp subdental ridge for its medial border. Below the subdental shelf, the Meckelian canal is restricted; its maximum depth is shallower than the lateral parapet of the tooth row. The specimen shows no indication of an intramandibular septum within the posterior part of the canal. The restricted Meckelian canal indicates that the splenial (not preserved) was probably narrow and

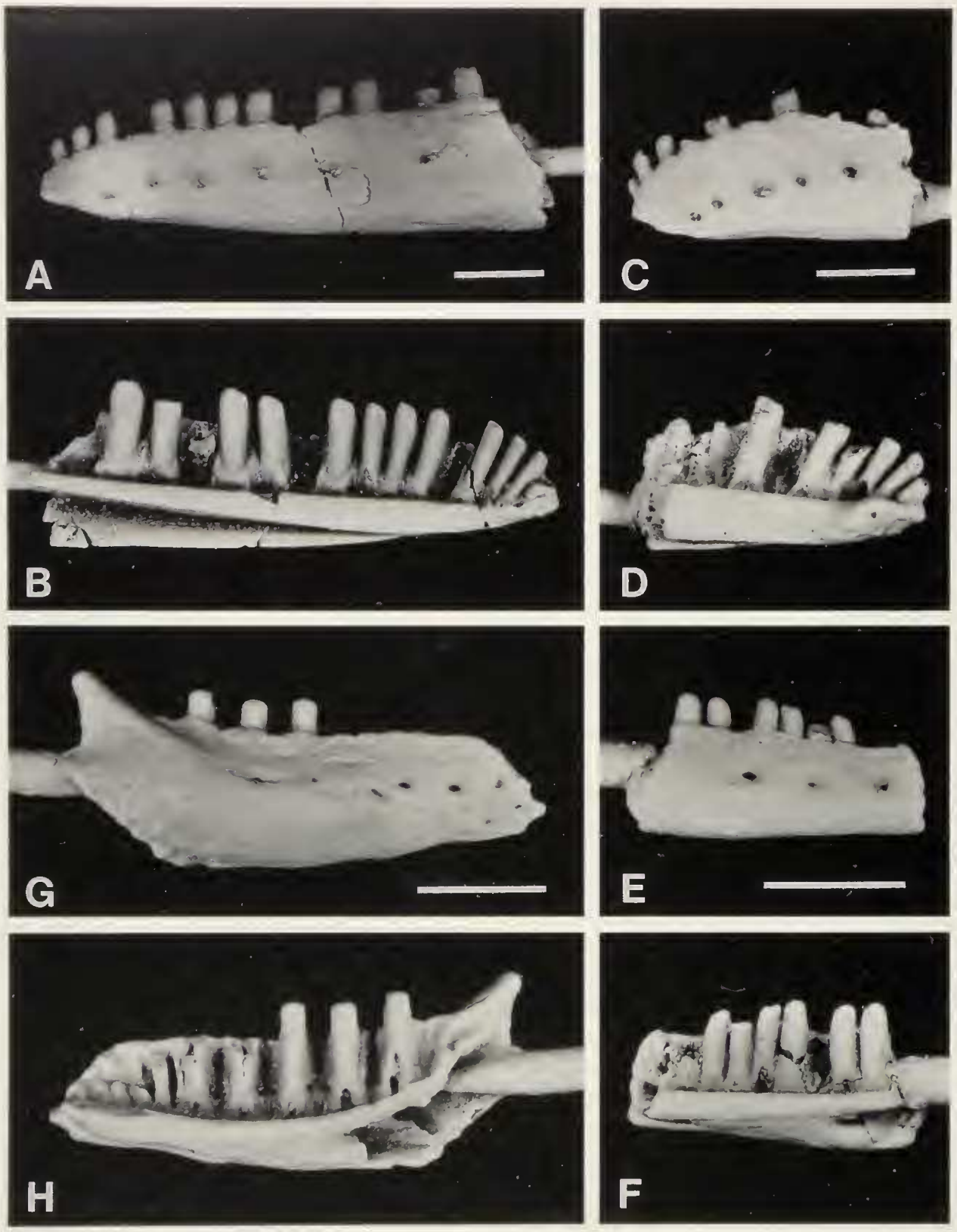

Fig. 24.—*Aocnodromeus corrugatus,* new genus and species, Milk River Formation, Alberta: A, B, UALVP 29905 (holotype), left dentary, lateral and medial views; C, D, UALVP 29906, left dentary fragment, lateral and medial views. ?Xantusiidae, new genus and species (unnamed), Hell Creek Formation, Montana: E, F, UALVP 29840, fragment of right mandible, lateral and medial views; *Contogenys sloani,* Hell Creek Formation, Montana: G, H, UALVP 29839, right mandible, lateral and medial views. Scale = 2 mm.

elongated, and the spleniodentary articulation terminated anteriorly below the seventh and eighth tooth positions. The referred specimen UALVP 29906 (Fig. 24C, D) is compatible in every respect with the holotype, except for its larger size.

The dentary teeth are widely spaced from one another and are pleurodont, with about two-thirds of their height attached to the lateral parapet of the dentary. The tooth shafts are solidly built and subcolumnar; even the anteriormost ones show little anteroposterior compression. Each tooth has a small basal foramen, while at least three (the eighth, the 11th, and the 14th) have developed a basal excavation for the replacing tooth posteromedial to the tooth base. The posteromedial location of these basal excavations indicates an "intermediate method" (Edmund, 1969) of tooth replacement for this lizard; only scincids combine this replacement pattern with the dentary and tooth morphology seen in *Aocnodromeus.* All of the dentary teeth that are preserved have their bases cemented to the dentary. The tooth crowns are medially concave and striated (see Fig. 23), with fainter striae labially. The anterior and middle teeth (the first 14) are unicuspid, with the tooth apex curved posteromedially to form an "in-

wardly pointing V" (Estes, 1964:125) in dorsal view; but the posterior teeth (the last five to seven) tend to be labiolingually compressed, and more or less molariform with truncate crowns. The lingual striations on these posterior teeth are also stronger than those on the anterior and middle teeth. This difference in crown pattern of the posterior teeth is clearly shown on the completely preserved 15th tooth on the holotype.

Discussion.—From the characters described above, the specimens UALVP 29905–29906 from the upper member of the Milk River Formation represent a new genus and species that can be placed in the Scincomorpha; this new lizard has a well-defined subdental shelf and a sulcus dentalis, and no indication of a vertically directed intramandibular septum. The familial affinities of this lizard are difficult to determine, because there are no reliable character states (synapomorphies at the familial level) shown on the holotype (the coronoid, an important structure, is broken off). Character states from the tooth morphology of this lizard (unicuspid crowns curved to form an "inwardly pointing V," medial striations, and small basal foramen) indicate affinity to the family Scincidae (see, e.g., Rowe et al., 1992, and Richter, 1994, for Cretaceous scincids with similar tooth morphology). But the robustness of the dentary and strong mandibular symphysis, especially the robust subdental shelf, are indicative of possible cordylid affinities. This new lizard is tentatively referred to the Scincidae, pending further study on more specimens to clarify its taxonomic affiliation.

Estes et al. (1988:226) cited Gauthier's (1982) recognition of medial striations on the tooth crowns as an anguid synapomorphy; in fact, Gauthier's (1982:19) original statement cited the combination of the "teeth with twisted, chisel-shaped, striated, unicuspid and obtusely-pointed crowns" as the synapomorphy. Nevertheless, the presence of medial striations on the tooth crowns also occurs in several scincomorphan families: Scincidae (e.g., *Eumeces*), Cordylidae (e.g., *Cordylus*), and in Xantusiidae (e.g., *Palaeoxantusia*). Presence of this character in the early scincoid *Aocnodromeus,* corroborated with other evidence from Cretaceous scincomorphans (this paper; Rowe et al., 1992; Richter, 1994), suggests that this character is symplesiomorphic for scincomorphans. Of course, the medial striations in Anguidae, especially in glyptosaurines, are much stronger than those in the other groups and are frequently associated with an obtuse, chisel-shaped cutting edge of the crown. The latter combination is obviously best designed for durophagous herbivorous feeding adaptations (Estes and Williams, 1984), functionally different from that in insectivorous or omnivorous scincids and others. Whether the presence of medial striations in the Anguidae is homologous to that in scincomorphans is still an open question.

The "inwardly pointing V" crown pattern recognized by Estes (1964) in some anguids is comparable to the problem concerning the medial striations: this morphology also occurs in some scincids, particularly those in the *Mabuya* group (personal observation). The occurrence of a similar crown pattern in the two phylogenetically remote groups is probably correlated with a similar food preference, and is thus convergent; it can be easily distinguished in the two groups by reference to other characters, such as jaw construction. Estes et al. (1988) argued that this kind of similarity does not invalidate the synapomorphic status of the "inwardly pointing V" crown pattern for the Anguidae, because the "inwardly pointing V" in the Anguidae and that in the Scincidae are not the same character in terms of origin, although they are the same in terms of morphology.

Family ?Xantusiidae Baird, 1859

The Xantusiidae or night lizards are small rock dwellers, which in many ways convergently resemble the geckos: most extant xantusiids are nocturnal insectivores with large eyes and fused eyelids, and their flattened body enables them to squeeze into narrow crevices (e.g., Mattison, 1989). The family has extant representatives of about 16 species in four genera (Savage, 1963), and a geographical distribution in North and Central America, including the West Indies. The phylogenetic relationships of the family have been controversial, as the group has been allied with scincomorphs by some authors (e.g., Camp, 1923; Romer, 1956; Moffat, 1973; Estes, 1983*a*) but with gekkotans by others (e.g., McDowell and Bogert, 1954; Savage, 1963; Northcutt, 1978). The most recent phylogenetic analysis strongly suggests a sister-group relationship with the Lacertiformes (Estes et al., 1988).

The evolutionary history of the Xantusiidae can be traced back to the Paleocene, as *Palaeoxantusia* Hecht, 1956, is closely related to the extant *Xantusia* (Hecht, 1956; Estes, 1983*a*). Three genera from the Upper Cretaceous of the Asian Gobi Desert (*Slavoia* Sulimski, 1984; *Eoxanta* and *Globaura* Borsuk-Bialynicka, 1988) show xantusiid affinities, but their relationships within the Scincomorpha have not been clarified. As discussed below, the North American fossil record includes possible xan-

tusiids that are Late Cretaceous in age. *Contogenys,* previously considered as an early scincid, is questionably assigned to the Xantusiidae, although a more definite referral to that family needs further study on better preserved specimens.

Genus and species new (unnamed)
(Fig. 24E, F)

Specimen.—UALVP 29840, fragmentary right mandible consisting of partially fused spleniodentary bearing six teeth and the bases for three others.

Locality and Horizon.—BCA locality, SW 1/4, Sec. 9, Tp. 22, R 43, McCone County, eastern Montana; Upper Cretaceous Hell Creek Formation (Lancian).

Description.—The specimen UALVP 29840 (Fig. 24E, F) is a small right spleniodentary having nine tooth positions preserved. Although incomplete, the dentary is short, probably bearing no more than 15 teeth originally. The lateral surface of the jaw is smooth, and shows three tiny lateral inferior alveolar foramina that are equally spaced from one another. The ventral border of the dentary is strongly turned medially, so that the ventral spleniodentary articulation (partially fused) is entirely medial to the ventral midline of the jaw. In medial view, the well-defined subdental shelf is at such a low position (similar to that in *Contogenys*) that the Meckelian canal is extremely restricted dorsoventrally. In cross section, exposed posteriorly where the dentary is broken, the Meckelian canal is just slightly wider than the more laterally located inferior alveolar canal. The splenial is greatly narrowed, but not retracted, is medioventrally located, and partially fused to the dentary along the ventral spleniodentary articulation below the anterior inferior alveolar foramen, which penetrates the splenial below probably the fourth or the fifth tooth position from the rear.

Although the general proportions of this specimen are similar to those of the dentary of *Contogenys,* the teeth are obviously different. The preserved part of the dentary bears nine tooth positions, including six teeth and the tooth bases for three others. These teeth are so closely spaced along the tooth row that little free space intervenes between successive teeth. The tooth attachment is pleurodont, with one-third of the tooth height projecting above the lateral parapet of dentary. The tooth shafts are cylindrical, lacking either anteroposterior compression or medial expansion. The crowns are nonstriated, and bluntly subconical, being somewhat compressed bilaterally and slightly recurved, with faint anterior and posterior lateral ridges. Two teeth on the jaw have developed deep resorption pits medially at the base, suggesting a direct replacement (Rieppel, 1978) or the "iguanid method" of tooth replacement (Edmund, 1969), in which the replacement teeth are developed directly at the bases of old teeth.

Discussion.—UALVP 29840 from the Hell Creek Formation represents a previously unknown lizard, which may be closely related to a *Contogenys*-like form occurring in the study area (see later discussion), and for this reason, this new specimen is included in this study. In terms of dentary structure and tooth form, the new specimen shows the following character states that may be taxonomically significant: short spleniodentary with the splenial greatly narrowed and partially fused to the dentary; a strong tendency to enclose the dentary tube by spleniodentary fusion; and pleurodont teeth having cylindrical shafts, with subconical and nonstriated crowns. However, UALVP 29840 is not complete enough to be the name-bearer of a new species; therefore, it is appropriate to leave the new genus and species unnamed until more, better preserved specimens are found.

The specimen UALVP 29840 shows a strong subdental shelf, a well-defined sulcus dentalis, and an indication of direct tooth replacement. These together are indicative of a scincomorphan relationship for this lizard. However, the familial affinities of this species are somewhat uncertain, as the spleniodentary is too incomplete to show reliable synapomorphies with a scincomorphan family. Both the shape of the dentary and the tooth form of this species show close similarities to those of *Palaeoxantusia* (see discussion below), indicating a possible affinity with the Xantusiidae. The partial fusion with the dentary of the greatly narrowed splenial shows a tendency to develop an enclosed dentary tube, which is characteristic of the Xantusiidae (see Estes et al., 1988). On the basis of these similarities, we tentatively classify this species in the Xantusiidae, until further study on more nearly complete specimens can clarify its taxonomic position.

The Tertiary *Palaeoxantusia* was originally named by Hecht (1956:4) as an Eocene "xantusiid lizard distinguished from the smaller members of the genus *Xantusia* by its smaller size, more robust dentary, its distinct splenio-dentary depression, and groove for the adductor mandibulae externus superficialis." At present, the genus has four species and a geologic range from middle Paleocene to lower Oligocene (see Schatzinger, 1975, 1980; Estes, 1983*a*). The type species *Palaeoxantusia fera* (Hecht, 1956) was founded on a nearly complete spleniodentary (holotype AMNH 3815) from the mid-Eocene Bridger Formation, Sublette County, Wyoming. The spleniodentary is short and robust, with 13 tooth positions. "The teeth are pleurodont, conical, robust, and rounded at the apex. Below the teeth on the internal surface there is a distinct shelf with a groove" (Hecht, 1956:5).

The specimen UALVP 29840 from the Hell Creek Formation shares several character states in jaw construction and tooth form with *Palaeoxantusia,* indicating its possible relationship to the Xantusiidae. However, UALVP 29840 differs from *Palaeoxantusia* in having a comparatively larger

splenial that is less extensively fused to the dentary, and in having the Meckelian canal open anteriorly. Our current knowledge on xantusiid evolution indicates that these are primitive character states within the family (Estes et al., 1988). According to Savage (1963), *Palaeoxantusia* is more primitive than *Xantusia* Baird, 1859, in morphology of the spleniodentary, and may represent the ancestral stock from which the latter form is derived.

From the available evidence, the newly discovered Hell Creek specimen is structurally more primitive than *Palaeoxantusia*. The ventral spleniodentary articulation below the anterior inferior alveolar foramen is clearly fused without a suture, and this fusion can be regarded as the initial step from a more primitive condition towards the complete fusion of spleniodentary and the enclosure of the dentary tube in the early evolution of the Xantusiidae. Therefore, UALVP 29840 may represent a basal taxon of the Xantusiidae, which in jaw structure is more primitive than *Palaeoxantusia* and *Xantusia*.

Genus *Contogenys* Estes, 1969*b*

Type Species.—*Contogenys sloani* Estes, 1969*b*.
Range.—Upper Cretaceous, North America.
Diagnosis.—As for the type species.

Contogenys sloani Estes, 1969*b*
(Fig. 24G, H)

Holotype.—MCZ 3681, nearly complete left dentary having five teeth and the spaces for ten others (see Estes, 1969*b*).

Paratypes.—MCZ 3682–3685, fragmentary maxillary and dentaries (Estes, 1969*b*).

Type Locality and Horizon.—BCA locality, SW 1/4, Sec. 9, Tp. 22, R 43, McCone County, eastern Montana; Upper Cretaceous Hell Creek Formation (Lancian).

Included Specimen.—UALVP 29839, topotypic right dentary collected by a UALVP field party in 1969. This specimen is included here because it provides new information for a taxonomic revision of *Contogenys sloani*; *C. sloani* appears to be phyletically close to a poorly known taxon from the study area (family incertae sedis, genus and species undetermined, see below).

Known Distribution.—Upper Cretaceous Hell Creek Formation, eastern Montana. The referrals of several Paleocene specimens (YPM-PU and AMNH specimens) to this taxon are unconvincing (see later discussion). There is also a recent report of specimens of this genus from Judithian beds of New Jersey (Denton et al., 1991), but a taxonomic description is as yet unpublished.

Diagnosis (Revised from Estes, 1983a).—A possible xantusiid of Late Cretaceous age, characterized by the following combination of character states: dentary short, with 16 or fewer teeth; tooth shafts anteroposteriorly compressed and medially expanded; tooth crowns truncate, having weak anteroposterior apical groove flanked by crests; inferior alveolar canal distinctively wider than Meckelian canal; dentary coronoid process strongly projecting posterodorsally.

Description.—Estes (1969*b*) has provided a sufficient description of the holotype (MCZ 3681) and the several Paleocene specimens. However, the newly collected topotypic specimen (UALVP 29839) reveals new information and provides the basis for emending the diagnosis of this taxon. Therefore, a description of the new specimen is necessary, in comparison with the original description of the holotype.

The dentary UALVP 29839 (Fig. 24G, H) has only the anterior tip and the posteroventral corner missing; otherwise it is complete. Like the holotype, the new specimen is extremely short and relatively deep, having 15 positions in the complete tooth row, including three complete teeth, bases for two more, and spaces for ten others. In medial view, the subdental shelf is at a position close to the ventral border of the jaw; the ventral position of the shelf, combined with the widening of the inferior alveolar canal, results in a great restriction of the Meckelian canal into an extremely narrow tube. The intramandibular septum is vertically directed but poorly developed, and has no free ventral border, differing from that in anguimorphans. The splenial, which is firmly articulated with the dentary, is greatly reduced dorsoventrally and terminates anteriorly below the sixth tooth position. The anterior inferior alveolar foramen penetrates the splenial below the fourth posteriormost tooth.

The subdental shelf curves posterodorsally, ending at the last dentary tooth; immediately behind this tooth and medial to the small but prominent coronoid process of the dentary is a distinct facet that receives the anteromedial process of the coronoid bone (Estes, 1969*b*), which is not preserved. The subdental shelf lacks a dorsal ridge, and the sulcus dentalis is poorly defined (contra Estes, 1969*b*). The dentary teeth are pleurodont, having one-third of their height projecting above the high lateral parapet of the jaw. The tooth shafts are strongly compressed anteroposteriorly, with a weak, shoulder-like, medial expansion. Small basal foramina that open medially are clearly shown at the tooth bases. The crowns are squared-off, more or less chisel-like, with slight lateral compression. There are no medial striations, but faint anterior and posterior ridges are developed.

The lateral surface of the dentary is strongly convex, reflecting the bulge of the inferior alveolar canal internally, which is wider than the greatly reduced Meckelian canal in posterior view. The coronoid process of the dentary is small, but prominent, and strongly projecting posterodorsally. Posterolateral to and below this process is a depression for the attachment of the adductor muscle, as in other xantusiids (Estes, 1969*b*). The posteroventral (Meckelian) process is broken off, but its large base indicates that the process is much stronger than, and extends posteriorly well beyond, the dorsal process. The lateral surface has a row of inferior alveolar foramina as seen in other lizards, but as a minor

individual variant, at least two extra foramina are developed anteriorly below the main row (the holotype MCZ 3681 shows a similar condition, see Estes, 1969*b*:fig. 1a).

Discussion.—Estes (1969*b*) founded *Contogenys sloani* on several specimens (maxillary, dentary, and parietal materials) from the BCA locality, and assigned the species to the family Scincidae. Estes (1969*b*) also referred several specimens (YPM-PU 17035, 17036*a*, 17036*b*) from the Paleocene Tongue River Formation, Montana, to this species. The results of this study show that both the classification of *C. sloani* in the Scincidae and the referral of the Paleocene YPM-PU specimens to this species are questionable. Sullivan's (1982) referral of a maxillary from the "Fort Union Formation" to this species is questionable as well, as it is based on an unreliable character.

Familial Assignment of *Contogenys*. The original classification of *Contogenys* in the Scincidae was determined largely "on the basis of the *Eumeces*-like wedge on the posterior border of the maxilla and on the general appearance of the teeth" (Estes, 1969*b*:5). However, the following observations indicate that the character states on which this placement is based are unreliable: first, the posterior extremity of the maxillary in primitive extant scincids (e.g., *Eumeces inexpectatus, Mabuya* sp.; personal observation, and see Estes et al., 1988:fig. 25, *Eumeces obsoletus*) is marked by an anteriorly directed triangular notch defined by two posteriorly directed processes, one dorsal, one ventral; the dorsal process fits into a triangular depression on the lateral surface of the jugal, so that the maxillary–jugal suture is actually Z-shaped in lateral view (personal observation). Contrary to Estes (1969*b*), there is no triangular wedge of the maxillary that inserts into the jugal in primitive skinks; instead, the jugal inserts into the maxillary notch. Second, while the enlarged "triangular wedge" on the maxillary in *Contogenys* (MCZ 3682) appears to be the homologue of the more dorsal of the two processes in scincids, the ventral process, defining the lower border of the notch in scincids (see above), is "absent" (Estes, 1983*a*:106). Lacking well-preserved specimens, we do not know the pattern of articulation between the maxillary and jugal in *Contogenys* other than it is not like that in primitive scincids; hence, the articulation between the maxillary and jugal cannot be invoked as evidence of the scincid affinities of *Contogenys*. Third, *Contogenys* has a short jaw with fewer, more or less chisel-shaped teeth, showing no resemblance to extant scincids (e.g., *Eumeces, Mabuya*), which have elongated jaws with numerous unicuspid teeth. In sum, therefore, Estes' (1983*b*:370) "*Eumeces*-like aspect" of *Contogenys* is questionable, and cannot be used to support referral of this lizard to the Scincidae. We also have discovered that at least some cordylids (e.g., UALVP unnumbered specimen, *Cordylus breyeri*) have a scincid-like articulation between the maxillary and jugal, effectively removing the basis for Estes' (1969*b*, 1983*a*, 1983*b*) argument.

In this study, we have compared *Contogenys* with the Tertiary *Palaeoxantusia* (see Hecht, 1956; Estes, 1983*a*); similarities between the two suggest that *Contogenys* is a xantusiid. They seem to share a unique jaw configuration and tooth form with extant xantusiids. They both have a short dentary with relatively few, more or less chisel-shaped teeth, each with a small basal foramen, and a small, but prominent, coronoid process of the dentary with a distinct posterodorsal facet (see Estes, 1983*a*:fig. 31B). In both *Contogenys* and *Palaeoxantusia,* the dentary has a posteroventral process (Meckelian process of Estes, 1969*b*) that is much stronger than, and extends posteriorly well beyond, the coronoid process of the dentary. This condition is in contrast with that of scincids, in which the two processes are more or less equally developed, but is similar to that of extant *Xantusia* (see Estes et al., 1988:fig. 21) and a possible early xantusiid, *Eoxanta* Borsuk-Bialynicka, 1988, from the Upper Cretaceous of the Gobi Desert. A large posteroventral process is also seen in Gekkonidae, Pygopodidae, Cordylidae, Paramacellodidae, and Amphisbaenia (personal observation). If this is a primitive feature, it is retained in the Xantusiidae but lost in the Scincidae. The only notable difference in dentary construction between *Contogenys* and *Palaeoxantusia* is the enclosed dentary tube in the latter; however, its Cretaceous relative might be expected to have an unfused dentary tube, but one showing the tendency towards fusion, as is the case with *Contogenys*. Furthermore, MCZ 3682, a paratype of *Contogenys* (Estes, 1969*b*:fig. 2; 1983*a*:fig. 26D), shows a distinct ventrally directed curvature at the posterior end of the supradental shelf. A similar condition is seen in extant *Xantusia,* but not in scincids *Eumeces* or *Mabuya* (personal observation). This adds another character state indicating the affinity of *Contogenys* to the Xantusiidae, not to the Scincidae.

As indicated in the above discussion, we have found no solid evidence that indicates association of *Contogenys* with the Scincidae, but have noted some resemblances to *Palaeoxantusia* and *Xantusia*. We believe that an enlarged posteroventral process

of the dentary and a posteroventral curvature of the supradental shelf are diagnostic features for a taxon that includes extant *Xantusia* and fossil *Palaeoxantusia* and *Contogenys,* that is, the Xantusiidae or the family plus its sister group *Contogenys.* Therefore, *Contogenys* is tentatively placed in the Xantusiidae in this paper, pending verification by a more extensive study of fossil and Recent materials.

The Problem of Paleocene *Contogenys*. The YPM-PU specimens referred to *Contogenys sloani* by Estes (1969*b*) are several dentaries from the mid-Paleocene Tongue River Formation, Montana. These specimens, as Estes (1969*b*:fig. 4) figured, seemingly differ from the holotype (MCZ 3681) and other Late Cretaceous specimens of *Contogenys* in having columnar teeth with large basal excavation, striated crowns, a more prominent subdental shelf, and a deeper Meckelian canal that indicates a larger splenial. All of these differences are beyond the range of individual variation from current understanding of the species. The short jaw with fewer teeth, and the nature of the coronoid and Meckelian processes of the dentary may suggest affinity with *Contogenys* at or above the generic level, but these specimens seem not referrable to *C. sloani.*

Sullivan (1982) identified AMNH 12069 (from the mid-Paleocene "Fort Union Formation," Wyoming) as a right maxillary, and referred it to "cf. *Contogenys sloani,*" which Estes later (1983*a*) listed as "cf. *Contogenys* sp." According to Sullivan (1982:999), the referral of this specimen to *Contogenys sloani* is based "on the evidence of an expansion of the maxilla posterolaterally that indicates the probable presence of a triangular wedge (as reported by Estes, 1969) as well as the presence of strongly pleurodont teeth with squared-off tooth crowns." The so-called "triangular wedge" is not a diagnostic feature for *Contogenys,* nor for the Scincidae, as discussed before. Another feature on which Sullivan's referral is based, "strongly pleurodont teeth with squared-off tooth crowns," is not unique to *Contogenys,* but shared with taxa in other families (e.g., Xantusiidae, Anguidae). Sullivan's (1982:text fig. 4) figure shows that the teeth on AMNH 12069 are not strongly anteroposteriorly compressed and lack a basal foramen, which is well developed in *Contogenys sloani.* The fragmentary nature of the specimen makes further comments difficult; however, in our view the specimen is, in both size and tooth form, indistinguishable from *Palaeoxantusia* from the same locality.

The Status of *Paracontogenys* Schatzinger ex Estes, 1983*a*. Schatzinger (1975) named *Paracontogenys estesi* in his unpublished thesis, based on several specimens from the upper Eocene Mission Valley Formation, San Diego, California. Golz and Lillegraven (1977) cited this name in a faunal list, although the description of the taxon had not yet been published (hence the name was not valid). Estes (1983*a*:110–111) figured the holotype (UCMP 113228), provided a diagnosis, description, and comments on the taxon, but cited the taxon name as "*Paracontogenys estesi* Schatzinger 1975 in Golz and Lillegraven 1977." Since Estes (1983*a*) is the first who made the name available and valid (ICZN, 1985), a correct citation of this name should be "*Paracontogenys estesi* Schatzinger ex Estes, 1983*a*."

Paracontogenys is diagnosed as a scincid differing from *Contogenys* in having a greater number of dentary teeth, a closed Meckelian canal, and medial striations on the tooth crowns (Schatzinger, 1975; Estes, 1983*a*). As Schatzinger (1975) noted, this Eocene lizard is closely similar to the Late Cretaceous *Contogenys*; however, as is the case with *Contogenys,* its familial placement in the Scincidae is questionable, as no diagnostic characters for Scincidae are shown on the specimens; it may pertain to the Xantusiidae.

Probably in respect to the faint medial striations on the tooth crowns as a taxonomically significant character, Estes (1983*a*:111) commented that "a reference [of *Paracontogenys*] to Xantusiidae is possible but improbable as tooth crown structure is more like scincids than xantusiids." Now it is clear that this character is shared by several scincomorphan families, and is also seen in some xantusiids (e.g., Schatzinger, 1980). This wide distribution of this character state, and its occurrence in Jurassic paramacellodids (see Estes, 1983*a*), suggests that possession of striations on the crown surface is probably symplesiomorphic for scincomorphans, but is not unique for the Scincidae. It seems to us that *Paracontogenys* is best referred to the Xantusiidae. The most indicative character of *Paracontogenys* in respect to its familial affinities is probably its short jaw, with the fusion of the dentary tube extending posteriorly close to the posterior end of tooth row. This is characteristically the xantusiid condition, but is different from that in the Scincidae, in which the dentary is elongate and only the anterior half of the tube is closed, with the posterior half covered by the splenial (personal observation).

In sum, neither *Contogenys* nor *Paracontogenys* are likely members of the Scincidae, but are probably referrable to the Xantusiidae. An incomplete

survey of dentary structure indicates that the two genera share with the Xantusiidae the following character states: (1) the posteroventral process (or Meckelian process) of the dentary is larger overall than the coronoid process of the dentary, (2) the posteroventral process of the dentary extends posteriorly well beyond the level of the dorsal coronoid process, (3) the coronoid process of the dentary medially has a distinctive facet behind the tooth row (Hecht, 1956). The first two character states are probably primitive at a higher taxon level, while the third is unambigiuously unique for the Xantusiidae.

Family ?Cordylidae Gray, 1837

The family Cordylidae, as defined by Romer (1956), consists of the Cordylinae and the Gerrhosaurinae, subgroups that were previously placed in two separate families (e.g., Camp, 1923). The Cordylidae include approximately 70 extant species in about ten genera, which are confined to Africa and Madagascar in their geographic distribution.

The monophyly of the Cordylidae by Romer's definition is supported by evidence from chromosomal analysis (Olmo and Odierna, 1980) and several anatomical synapomorphies (Estes et al., 1988), but the relationships of this family with the Jurassic Paramacellodidae Estes, 1983*a*, are still unclear. If the latter group stands as a separate family, the Cordylidae have no definite North American Mesozoic record, with Late Cretaceous taxa referred to it only with uncertainty (*Sauriscus* Estes, 1964, and undetermined taxa in this paper). Recent discoveries of Mesozoic lizard osteoderms from the Upper Cretaceous of Madagascar document a possible early cordylid record outside North America (Gao, 1994).

Genus and species undetermined (A) (Fig. 25A, B)

Specimens.—UALVP 29810, dentary fragment with four teeth, and the broken bases and spaces for eight others; UALVP 29907, dentary fragment with the bases and spaces for ten teeth.

Locality and Horizon.—Outcrop of the Oldman Formation near Irvine, in Sec. 31, Tp. 11, R 2, W 4, about 40 km east of Medicine Hat, southeastern Alberta; Upper Cretaceous Oldman Formation (Judithian).

Description.—Of the two specimens above, UALVP 29810 (Fig. 25A) is the better preserved, having four teeth in place, while those on UALVP 29907 are all broken off. What remains of the dentary of UALVP 29810 is short and robust; the breakage is at the 12th tooth position, so that its posterior end, especially the taxonomically important coronoid process, is not preserved. The dentary bears a robust subdental shelf, the maximum depth of which is about half of the tooth height. The depth and the robustness of the shelf remain unchanged below the first eight tooth positions, but the shelf is reduced posteriorly from the ninth position, where the anterodorsal spleniodentary articulation terminates (judging from the articular scar on the specimen) and the Meckelian canal becomes deeper and faces more medially. The subdental shelf dorsally bears a shallow but clearly defined sulcus dentalis, along the medial side of the tooth row. The lateral surface of the dentary is smooth, slightly convex, and has small inferior alveolar foramina that are unevenly spaced from one another. The posterior foramina tend to be closer to the upper rim of the jaw.

Among the four teeth preserved on UALVP 29810, two (the sixth and the eighth) are complete, and the other two (the fourth and the fifth) have the bases and the shafts preserved but the crowns are broken off. The teeth are pleurodont, with the upper one-third of the tooth height projecting above the lateral parapet of the jaw. The tooth shafts, closely spaced along the tooth row, are strongly compressed anteroposteriorly, but lack a shoulder-like medial expansion. Both of the complete teeth have developed a basal cavity, and in another tooth (the fifth), the lower half of the tooth has been resorbed. These indicate that the tooth replacement of this lizard is direct or by the so-called "iguanid method" (Edmund, 1969), which is also seen in extant cordylids. The tooth crowns are unicuspid with a blunt, inwardly curved cusp and clearly defined anterior and posterior vertical ridges. The crowns show no indication of lateral compression, no tendency towards becoming chisel-like, and lack striae on both the medial and lateral surfaces.

The second specimen (UALVP 29907; Fig. 25B) shows the same proportions as UALVP 29810, but is obviously more slender in correspondence with its smaller size. The teeth are all broken off, but the tooth bases clearly show that the teeth were strongly compressed anteroposteriorly, and were closely packed along the tooth row, as in UALVP 29810. This specimen shows that the posterior interior alveolar foramen opens into the Meckelian canal close to the posterior end of the tooth row, but there is no indication of a vertically directed intramandibular septum.

Discussion.—The two specimens described above represent a previously unknown fossil scincomorphan taxon. This taxon remains unnamed in this paper, because the two specimens are not complete enough to provide an adequate diagnosis of a new genus and species. The familial assignment of this lizard is difficult from the evidence at hand; however, the shape of the dentary and the tooth form suggest possible affinities with the family Cordylidae. The dentary is closely similar to that of *Saurillodon* Estes, 1983*a*, an Upper Jurassic scincomorphan from Portugal that Seiffert (1973) put in the Scincidae but Estes (1983*a*) put in the Paramacellodidae Estes, 1983*a*. In both the dentary is short, with a low number of teeth and a characteristically robust subdental shelf. However, the new lizard from the Oldman Formation cannot be assigned to *Saurillodon* because of differences in tooth form supported by significant differences in geological age and geographical distribution. *Saur-*

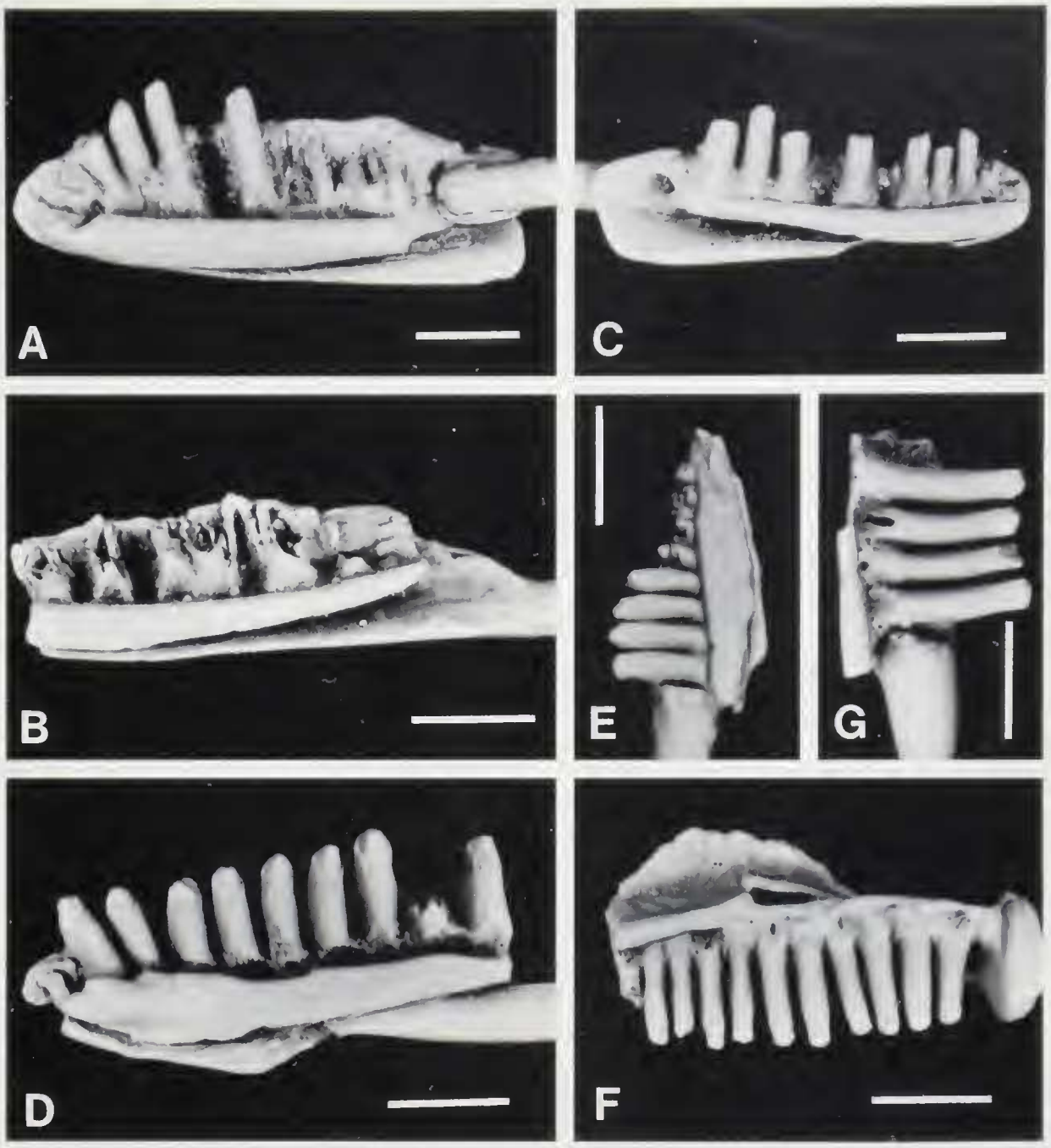

Fig. 25.—?Cordylidae, genus and species undetermined (A), Oldman Formation, Alberta: A, UALVP 29810, incomplete right dentary, medial view; B, UALVP 29907, incomplete right dentary, medial view. ?Cordylidae, genus and species undetermined (B), Hell Creek Formation, Montana: C, UALVP 29722, incomplete left dentary, medial view. Family incertae sedis, new genus and species (A), Frenchman Formation, Saskatchewan: D, SMNH P1927.880, incomplete right dentary, medial view. Family incertae sedis, new genus and species (B), Frenchman Formation, Saskatchewan: E, SMNH P1927.886, anterior part of left dentary, medial view. Family incertae sedis, genus and species undetermined, Milk River and Oldman formations, Alberta: F, UALVP 29830, incomplete right maxillary, medial view; G, RTMP 85.36.275, left dentary fragment, medial view. Scale = 1.5 mm.

illodon has conical teeth with columnar shafts, while the compressed shaft, obtuse crown, and lateral ridges on the teeth in the new lizard resemble corresponding parts of the teeth of extant *Cordylus*. The family Paramacellodidae, as a primitive group, is closely related to the Cordylidae, and may be a possible synonym of the latter (Estes, 1983*a*).

The similar proportions of the dentary of the Oldman species and the Jurassic *Saurillodon* could be regarded as a primitive character for cordylids, but the similarity to *Cordylus* in tooth morphology and a rather straight ventral border of the dentary are probably more indicative of its familial affinity. Other evidence concerning the splenial supports this interpretation: although the splenial is not preserved on either UALVP 29810 or 29907, a scar shows that the dorsal spleniodentary articulation terminated anteriorly close to the midpoint of the tooth row. Similar proportions are seen in extant *Cordylus* (personal observation), while Jurassic *Saurillodon* shows a more anterior, presumably primitive, extension of the splenial.

Genus and species undetermined (B)
(Fig. 25C)

Specimen.—UALVP 29722, incomplete left dentary having seven teeth and the bases and spaces for four others.

Locality and Horizon.—BCA locality, McCone County, eastern Montana; Upper Cretaceous Hell Creek Formation (Lancian).

Description.—UALVP 29722 (Fig. 25C) is a short, shallow, and lightly built left dentary with 11 tooth positions preserved. The anterior end of the bone is slightly rounded by erosion, with probably only the first tooth missing. The dentary is posteriorly broken close to the end of the tooth row, as the subdental shelf is greatly diminished corresponding to the termination of the tooth row. The lateral surface of the dentary is smooth, and is gently convex. Unlike UALVP 29810 (genus and species undetermined A) described above, this specimen has only three small inferior alveolar foramina on the lateral surface of the jaw, and these foramina are widely spaced from each other.

In medial view, the subdental shelf is anteriorly deep and robust below the first six teeth, but abruptly reduced posteriorly from the seventh tooth position. The maximum depth of the shelf is about half of the tooth height. The ventral edge of the shelf has a shallow but clearly defined groove for the dorsal spleniodentary articulation, and this groove terminates anteriorly below the seventh tooth position. The Meckelian canal is extremely narrow and open ventrally below the first seven teeth, but is greatly deepened posteriorly corresponding to the posterior diminishing of the subdental shelf. The maximum depth of the canal at its posterior end slightly exceeds the height of the lateral parapet of the dentary. The sulcus dentalis is so poorly developed that it is barely recognizable.

The dentary retains seven teeth and the bases of four others, in total representing the second through 12th positions of the dentary tooth row. Most of the teeth have the crowns broken off, but the 11th tooth (the only well-preserved tooth on the specimen) clearly shows a blunt, almost rounded central cusp, and faintly developed side cusps. The first three teeth are slightly compressed anteroposteriorly; the remainder are generally pillar-like, with a narrow crown but thickened shaft. Several broken teeth show a round cross section, with a thick tooth wall and thin tube-like pulp cavity. A deposit of cementum can be seen around the tooth bases, but this is far less than seen in teiids. On this specimen, only the third tooth has an excavation at the medial side of the tooth base; the rest show no sign of replacement cavities. The teeth are pleurodont, having the lower half or more of the teeth attached to the lateral parapet of the jaw.

Discussion.—The specimen UALVP 29722 from the Hell Creek Formation represents a lizard that may be closely related to "genus and species undetermined A" from the Oldman Formation (UALVP 29810); for this reason, this Hell Creek specimen is included in this study. These two forms share close similarities in the configuration of the dentary (short dentary, robust subdental shelf, and extremely narrow Meckelian canal) and the mode of tooth attachment, but the Hell Creek form B differs from the Oldman form A in having cylindrical tooth shafts, an incipiently tricuspid crown pattern, and poor development of the sulcus dentalis. The morphologic differences between the two forms (corroborated with their geologic age differences) indicate that they may pertain, at least, to two different species.

Family incertae sedis
Genus and species new (A)
(Fig. 25D)

Specimen.—SMNH P1927.880, incomplete right dentary bearing eight well-preserved teeth and the broken bases of two others.

Locality and Horizon.—Gryde locality, in Sec. 19, Tp. 4, R 18, W 3, Frenchman River Valley, southwestern Saskatchewan; Upper Cretaceous Frenchman Formation (Lancian).

Description.—The specimen SMNH P1927.880 (Fig. 25D) is the anterior half of a right dentary, which is broken immediately behind the tenth tooth, and also posteroventrally at the Meckelian canal. The specimen shows no indication of erosion through transportation, but displays several tooth marks, probably from a sharp-toothed predatory lizard or a small mammal.

Medially, the dentary bears a robust subdental shelf, which is anteriorly nearly as deep as the height of the teeth but sharply diminishes posteriorly. The shelf has a sharp subdental ridge, which medially borders a narrow and deep sulcus dentalis along the tooth row. The mandibular symphysis is strong, with a robust symphysial process. The Meckelian canal is greatly narrowed anteriorly, to a fissure-like opening under the first four tooth positions, and is widened posteriorly, corresponding to the deepening of the jaw and the diminishing of the subdental shelf; however, the canal is not as widely open as in teiids, which have an hypertrophied splenial.

The specimen has eight well-preserved teeth and the broken bases of two others, representing the first ten positions of the complete dentary tooth row. The teeth are pleurodont, and the lateral parapet is well developed to about half of the tooth height. Most of the teeth show a deep basal excavation, with part of the tooth base already having been resorbed. This type of basal excavation implies a direct tooth replacement pattern (Edmund, 1969). The tooth shafts are anteroposteriorly compressed for the first three or four teeth, but become increasingly pillar-like towards the posterior end of the tooth row. The tooth crowns are bluntly conical, with a weak crest (or ridge) encircling the crown surface, and are faintly striated on the medial surface.

In lateral view, the dentary is more or less wedge-shaped, having the horizontal dorsal border diverging posteriorly from the ventral border at an angle of 40–45 degrees. This particular jaw configuration to some extent resembles that of some Jurassic paramacellodids (e.g., *Becklesius*, see Estes, 1983*a*:fig. 28). The lateral surface has five inferior alveolar foramina that are small and rounded. The first four are equally spaced from one another, but the fifth is separated from the fourth by a space twice the length of those between the more anterior foramina.

Discussion.—As described above, SMNH P1927.880 has a well-developed subdental shelf and sulcus dentalis, and a relatively large splenial as in-

dicated by the open Meckelian canal. On the basis of these characters, this lizard can be placed confidently in the infraorder Scincomorpha; however, its familial relationships cannot be determined at present, because no synapomorphic character states can be clearly recognized in this specimen. Nevertheless, this new Lancian lizard differs from members of the Teiidae (one of the most common North American Late Cretaceous scincomorphan groups) in having a less heavy deposit of basal cementum, and a different tooth replacement pattern, as shown by deep and large basal excavations (compared to subcircular replacement pits in teiids). Instead, both the general jaw construction and the tooth form of this new lizard closely resemble those of *Becklesius hoffstetteri* (see Estes, 1983*a*:fig. 28), which is currently classified in the family Paramacellodidae (Estes, 1983*a*). Paramacellodids are known only from the Upper Jurassic of Europe, particularly from England and Portugal, and are possibly a paraphyletic group with exclusion of cordylids (Estes, 1983*a*). Both the geologic and geographic distributions of paramacellodids seem to hinder the referral of this species to the family. However, the above-mentioned similarities shed some light on the possible affinity of SMNH P1927.880 to the family Cordylidae, since the close relationship of Paramacellodidae with Cordylidae has been suggested by resemblances in mandibular construction and osteodermal morphology (Estes, 1983*a*). These similarities are so strong that Estes (1983*a*) predicted that "it is possible that the Paramacellodidae will prove a synonym of the Cordylidae" (Estes, 1983*a*:115).

Nevertheless, it appears that SMNH P1927.880 represents a new taxon, which may have a relationship with the Cordylidae. However, we here leave the taxon unnamed and classify it as "family incertae sedis," since the specimen is too incomplete to be designated as a holotype and its affiliation to the Cordylidae is less certain than the two questionable cordylid taxa described above.

Genus and species new (B)
(Fig. 25E)

Specimen.—SMNH P1927.886, P2004.90, both fragmentary dentaries having several teeth and broken bases preserved.

Locality and Horizon.—Gryde locality, in Sec. 19, Tp. 14, R 18, W 3, Frenchman River Valley, southwestern Saskatchewan; Upper Cretaceous Frenchman Formation (Lancian).

Description.—SMNH P1927.886 (Fig. 25E) is a fragmentary left dentary, which was probably originally short and deep, but quite robustly built in relation to its small size. The subdental shelf is mediolaterally narrow but dorsoventrally deep below the first eight tooth positions. This part of the subdental shelf is so deep that the ventral edge of the shelf is brought close to the ventral border of the jaw, depressing the anterior part of the Meckelian canal to form an extremely shallow and narrow ventral groove. The shelf posterior to this part is abruptly reduced in depth above what must have been a small splenial. The shelf has a subdental ridge that forms the medial border of the narrow but deep sulcus dentalis. The dentary is anteriorly pointed, indicating a weak mandibular symphysis.

SMNH P1927.886 has four teeth and the broken bases of six others preserved, representing the first ten positions of the complete tooth row. The teeth are high-crowned, closely spaced, and pleurodont, with the lower half of the tooth height attaching to the lateral parapet of the jaw. The tooth shafts are slender and cylindrical, neither compressed nor expanded. The tooth bases are clearly exposed and lack the heavy deposit of cementum seen in teiids. The bases also show no resorption pits or excavation. The crowns can be described as "incipiently tricuspid," as the crown of the ninth tooth has a prominent central cusp and faint side cusps. The posterior cusp is slightly stronger than the anterior one.

The lateral surface of the dentary shows five inferior alveolar foramina, and these foramina are about equal in size and in spacing from one another. Like SMNH P1927.880 (unnamed taxon A, described above), this dentary also shows tooth marks on both the medial and lateral sides of the jaw. Another specimen (SMNH P2004.90) is a left dentary fragment with four complete teeth. It is more fragmentary than P1927.886, but is referrable to the same species on the basis of its close resemblances in crown pattern, tooth attachment, and the robustness of the subdental shelf.

Discussion.—The two specimens described above represent a new genus and species, which is possibly referrable to the Cordylidae. Owing to the poor preservation of the specimens, the new taxon is unnamed, and hence, no holotype is designated and no diagnosis is presented. However, the unnamed taxon B seems to be different from taxon A above primarily in having high-crowned, closely compact, and incipiently tricuspid teeth, and in having a narrower Meckelian canal, besides its substantially smaller size. These differences may be counted as character states that separate the two lizards at the generic level. However, similarities in general shape of the jaw, robustness of the subdental shelf, and the nature of the sulcus dentalis suggest that the two taxa should be placed in the same family, either Cordylidae or Paramacellodidae.

As does SMNH P1927.880 (unnamed taxon A, see above), SMNH P1927.886 also shows a paleoecologically significant feature of tooth marks, probably indicative of predation or post-mortem scavenging in a subaerial environment. In addition, the breakage of the first six teeth on the jaw seems to

have happened before fossilization, also implying action by a predator or scavenger.

Genus and species undetermined (Fig. 25F, G)

Specimens.—Milk River Formation, MR-4 locality: UALVP 29830, incomplete right maxillary having ten teeth preserved; Oldman Formation, BB 78 (DPP): RTMP 85.36.275, fragmentary left dentary having four teeth preserved.

Description .—UALVP 29830 (Fig. 25F) consists of an incomplete right maxillary having ten teeth preserved. Although the dorsal process of the maxillary is broken, it shows a sharply descending posterior border, indicating a much shallower posterior part of the bone. Medially above the tooth row, the supradental shelf is obviously wider posteriorly than anteriorly, indicating a prominent palatine process. A large posterior interior alveolar foramen opens close to the midpoint of the tooth row.

The maxillary teeth are pleurodont, with the upper half of the teeth attached to the lateral parapet of the jaw. The tooth shafts are strongly compressed anteroposteriorly, giving them a triangular shape in anterior or posterior view. Although strongly compressed, the tooth shafts lack a shoulder-like medial expansion. There are no foramina at the tooth bases; instead, several teeth have developed a basal excavation for tooth replacement. The tooth crowns are partially dissolved on this specimen, but enough remains to show that the crowns were more or less chisel-shaped originally, with faint lateral crests. The anterior maxillary teeth are slightly shorter and more slender than the posterior ones.

RTMP 85.36.275 (Fig. 25G) is the posteriormost part of a left dentary, as indicated by its greatly diminished posterior end of the subdental shelf. The dentary fragment has four teeth preserved, and the teeth are similar to those on UALVP 29830: they are slightly compressed laterally, more or less chisel-shaped, and have faint anterior and posterior ridges running vertically on the medial side of the crowns. There are no striations on the crown surface. Differences in crown height and other characters suggest that the two specimens may not pertain to the same species; however, this possibility cannot be verified at this stage, owing to the fragmentary nature of the specimens.

Discussion.—The two specimens described above were collected from two localities at different geological horizons. They are lumped together as "genus and species undetermined" on the basis of their general resemblances in having anteroposteriorly compressed tooth shafts, and more or less chisel-like crowns without striations. These features are *Contogenys*-like, but poor preservation of the two specimens does not allow a reliable taxonomic referral, even at a familial level. However, the two specimens may not pertain to the same taxon, as RTMP 85.36.275 has taller, and more strongly compressed teeth than does UALVP 29830. They also differ from each other in tooth attachment: RTMP 85.36.275 has half, while UALVP 29830 has one-third, of its tooth height projecting over the parapet of the jaw. Nevertheless, the two poorly preserved specimens are inadequate for us to clearly distinguish them from one another, and to make a reasonable taxonomic assignment. Here, we place them together as "genus and species undetermined," pending further study on more and better preserved specimens to clarify their taxonomic position.

Infraorder Anguimorpha Fürbringer, 1900
Family Xenosauridae Cope, 1886

The family Xenosauridae includes the living species of Central American *Xenosaurus* and Asian *Shinisaurus* (McDowell and Bogert, 1954; Estes et al., 1988). Both the skull osteology and the natural history of the two genera are still poorly known; and the monophyly of the family, although supported by 12 synapomorphies (Estes et al., 1988), is still obscured by the wide geographic separation and distinct adaptations of the two genera (Gauthier, 1982; Pregill et al., 1986).

The Xenosauridae have a poor fossil record compared with other anguimorphan families. With the exclusion of *Nordenosaurus* Holman, 1973, from Squamata (Gauthier, 1982), there are only three species in two genera of fossil xenosaurids known from North America (Estes, 1983*a*). In addition, undescribed materials were recently reported from New Jersey (Denton et al., 1991). Several fossil taxa from the Gobi Desert also show xenosaurid affinities (Borsuk-Bialynicka, 1985, 1986), but further study is needed to clarify their relationships. In this paper, new specimens from the Lance and Hell Creek formations provide important materials for a better understanding of *Exostinus* Cope, 1873; several specimens from the Milk River Formation represent by far the earliest North American fossil record of this family, and may provide materials for future recognition of a new taxon.

Exostinus lancensis Gilmore, 1928 (Fig. 26, 27A–F)

Exostinus? lancensis Gilmore, 1928:23, pl. 26, fig. 2.
Harpagosaurus parvus Gilmore, 1928:156, fig. 98.
Prionosaurus regularis Gilmore, 1928:159, pl. 26, fig. 1.

Included Specimens.—Lance Formation, BTB locality: UALVP 29847, parietal; UALVP 29849–29850, incomplete maxillaries; UALVP 29838, dentary; UALVP 29920, jugal. AB locality: UALVP 29848, parietal. Hell Creek Formation, BCA locality: UALVP 29919, frontal. Although collected from outside the study area, these specimens are included in this paper because they represent an important but poorly known North American xenosaurid, which is closely related to the Oldman and Milk River forms known from the study area (see later description).

Known Distribution.—Upper Cretaceous Lance

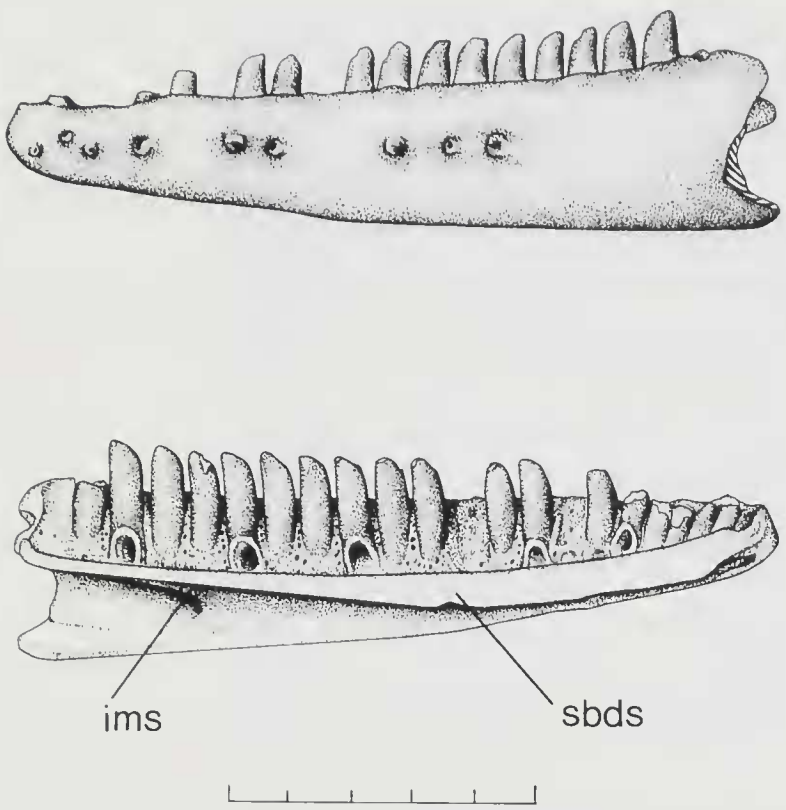

Fig. 26.—*Exostinus lancensis,* Lance Formation, Wyoming: UALVP 29838, nearly complete left dentary, lateral (above) and medial (below) views. Scale = 5 mm. Abbreviations as in Fig. 2.

Formation, eastern Wyoming; Hell Creek Formation, eastern Montana (all Lancian).

Diagnosis (Revised from Estes, 1983a).—A Late Cretaceous xenosaurid from North America, differing from the Oligocene *Exostinus serratus* by the following combination of character states: prefrontal incision of frontal not extending to midpoint of orbit; subdental shelf well defined, sulcus dentalis present; intramandibular septum less extensive posteriorly; posterior interior alveolar foramen more anteriorly located.

Description.—Gilmore (1928) described the holotype maxillary (USNM 10689), and Estes (1964) briefly described the dentary specimens of *Exostinus lancensis.* Newly discovered specimens from the Lance and Hell Creek formations include a frontal, a jugal, and the anterior end of a maxillary, parts that previously were unknown for this species. These specimens provide important information for a better understanding of this fossil xenosaurid, and hence are described below.

Maxillary. Two maxillaries (UALVP 29849, 29850), both from the Lance Formation, are referrable to *Exostinus lancensis* on the basis of their tooth form and the sculpture on the lateral surface. UALVP 29849 is the anterior part of a right maxillary, having six tooth positions preserved. The lateral surface of the maxillary is extensively ornamented with flattened patches of vermiculate sculpture that are separated by shallow grooves (Fig. 27A). At the lower border of the sculpture, the superior alveolar foramina are small and circular, as in the holotype (USNM 10689; see Estes, 1964). The maxillary has a prominent premaxillary process, behind which the vertical nasal process is slightly notched for the posterior border of the external narial opening; it then gently turns posterodorsally. In medial view, the vomerine process of the maxillary is stronger than the premaxillary process and is somewhat plate-like, with its widened base as the anterior extension of the supradental shelf. This medial process diverges from the lateral premaxillary process at a 45-degree angle. The supradental shelf is clearly defined, and a slight supradental gutter can be seen.

The six tooth positions preserved consist of five teeth and the space for another. Most of the teeth are broken, but the third is complete, showing that the crown is unicuspid, slightly recurved, and has a longer and trenchant anterior cutting edge; no striations are present. The tooth shafts are subcylindrical and thick-walled, and the tooth bases are firmly cemented to the lateral parapet. These teeth are pleurodont, having about two-thirds of their height attached to the parapet. Of the five teeth preserved, three clearly show a resorption cavity. The third tooth has almost half of its base resorbed, indicating a direct replacement mode (in agreement with Estes, 1964; but in conflict with McDowell and Bogert, 1954, who stated that xenosaurs have interdental replacement).

Another specimen, UALVP 29850 (Fig. 27B), is the posterior end of a left maxillary, which is broken at the posterior interior alveolar foramen in front of the fifth tooth position from the back. Although fragmentary, this specimen shows the same tooth morphology and osteodermal ornamentation as the holotype maxillary described and figured in Gilmore (1928). This fragment also preserves a structure unknown from other specimens: the posteriormost part of the supradental shelf develops a sigmoid twist, and the last two maxillary teeth are sharply reduced in size corresponding to the twist of the shelf (see Fig. 27B). This downward twist of the shelf seems to have a function in enhancing the maxillary–jugal articulation.

Frontal. UALVP 29919, a fragmentary frontal (Fig. 27C) from the Hell Creek Formation, is clearly referrable to *Exostinus lancensis,* as it is fused along the midline and hourglass-shaped, and is ornamented with vermiculate osteoderms. This frontal differs from that of *Restes rugosus* (Gilmore, 1942*a*) in having a prominent crust of tuberculate osteoderms (rather than flattened tesserae), and differs from that of *Exostinus serratus* Cope, 1873 (type species) in having larger and fewer tuberculate osteoderms, with a less complex surface texture. The ventral view of the specimen shows that the frontal fusion is complete, with the midline suture barely recognizable. The right subolfactory process is entirely broken off, but the left side indicates that the two processes tend to meet at the ventral midline and hold a trough-like subolfactory tract. In lateral view, the left anterior corner of the bone has a clearly defined prefrontal incision, the posterior extension of which does not reach the midpoint of the orbit.

Parietal. Two parietals (UALVP 29847 from the BTB locality and UALVP 29848 from the AB locality) are referred to *Exostinus lancensis,* both having osteodermal sculpture that is similar to the holotype maxillary; presence of "vermiculate sculpture" is a synapomorphy of the Xenosauridae (Estes et al., 1988). UALVP 29847 (Fig. 27D) shows a widened lateral border, implying suppression of the supratemporal opening and a short supratemporal process. UALVP 29848 shows that the parietal is a fused, single unit. Both specimens have osteodermal ornamentation that is heavy anteriorly but diminished posteriorly.

Jugal. UALVP 29920 (Fig. 27E) from the Lance Formation is the only jugal known that can be referred to *Exostinus lancensis.* The large size of this jugal indicates an individual larger than those represented by the other elements referred to this species, but it is of a characteristically xenosaurid type, with the postorbital branch widened and sculptured. The sculpture pattern

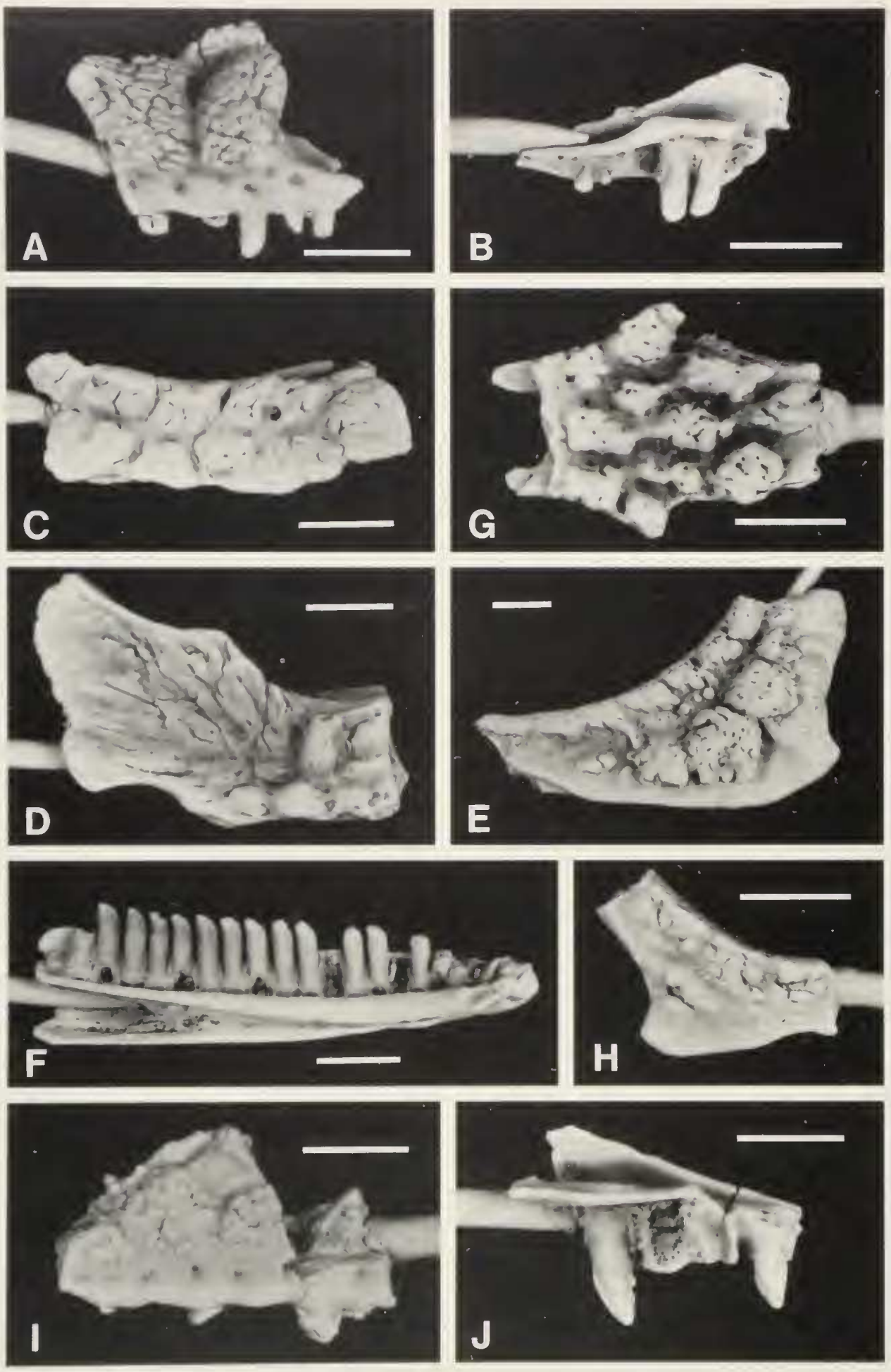

Fig. 27.—*Exostinus lancensis*, Lance and Hell Creek formations, Wyoming and Montana: A, UALVP 29849, incomplete right maxillary, lateral view; B, UALVP 29850, fragment of left maxillary, medial view; C, UALVP 29919, incomplete frontal, dorsal view; D, UALVP 29847, incomplete parietal, dorsal view; E, UALVP 29920, left jugal, lateral view; F, UALVP 29838, nearly complete left dentary, medial view. ?*Exostinus* sp., Oldman Formation, Alberta: G, UALVP 944, fragment of fused frontal, dorsal view. Xenosauridae, genus and species undetermined, Milk River Formation, Alberta: H, UALVP 29914, incomplete right jugal, lateral view; I, UALVP 29915, left maxillary fragment, lateral view; J, UALVP 29917, right maxillary fragment, medial view. Scale = 2 mm.

matches that on the frontal and parietals; therefore, these disarticulated specimens can be referred to the same species in spite of their size differences. The jugal is large, wide, and heavily ornamented with tuberculate osteodermal mounds on the lateral surface. Similar, but much smaller, osteodermal mounds coalesce along the posterior and ventral border of the orbit. The anteroventral process is elongated and thickened, forming most of the ventral border of the orbit. Although incomplete, the anterior end of this process bears a ventral crest, which fits into the posterior groove of the maxillary above the supradental shelf. The dorsal process of the jugal is largely broken off, but the base shows that it was widened and extensively ornamented (a synapomorphy of the Xenosauridae, see Estes et al., 1988).

Dentary. The dentary structure of *Exostinus lancensis* is not well known, except for Estes' (1964) brief description. UALVP 29838 (Fig. 26, 27F) from the BTB locality represents by far the most nearly complete dentary for this species, and provides the basis for a more extensive description of the dentary than was possible before. The dentary is elongate, lightly built, and relatively straight in dorsal view. The lateral surface is smooth and only weakly convex at the posterior part of the bone. Nine unequally spaced inferior alveolar foramina open laterally, with the posteriormost one located lateral to the 15th tooth position. Medially, it bears a horizontally straight, slender, but clearly defined subdental shelf, which has a subdental ridge bordering a shallow sulcus dentalis. The shelf gradually increases in depth anteriorly, and reaches a maximum depth about one-third of the tooth height. The Meckelian canal is anteriorly narrow and open ventrally below the first eight tooth positions; it increases in depth and width posteriorly, indicating that a splenial covered the most ventromedial aspect of the dentary. The maximum depth of the Meckelian canal is about equal to the tooth height. Both dorsal and ventral spleniodentary articulation surfaces terminate anteriorly under the ninth tooth position. The large posterior interior alveolar foramen opens into the Meckelian canal under the 18th and 19th teeth. As Gauthier (1982) has noted, this location is more anterior than that in the Oligocene *Exostinus serratus*. The intramandibular septum (sensu Estes et al., 1988) retains a primitive configuration: the septum is obliquely directed and lacks a free ventral border. This condition is similar to that in extant *Xenosaurus grandis* (see Gauthier, 1982:fig. 44) and some skinks (e.g., *Mabuya macularia*, personal observation), but is different from that in advanced anguids, in which the septum is vertically directed and has a free ventral border (Estes, 1964).

The dentary contains a nearly complete tooth row, consisting of 22 tooth positions (12 well-preserved teeth and tooth bases as well as spaces for ten others). We estimate that only the last one or two teeth are missing. The dentary teeth are closely spaced and pleurodont, with slightly less than one-third of the tooth height projecting above the lateral parapet. The tooth shafts are subcylindrical, lacking either compression or expansion. The tooth crowns are slightly compressed laterally and recurved, with the leading cutting edge much longer than the posterior one, giving the teeth a dagger-like appearance. The crowns are not serrated along the cutting edge, but they are faintly striated on the medial surfaces of at least some teeth (in agreement with Estes [1964], who described the teeth as having "faint lingual striations"). Although several teeth have their anterior cutting edge chipped, as if they were "bicuspid," well-preserved teeth clearly show no indication of a second cusp or cuspule on the crowns. This observation is contrary to Estes (1964) and Gauthier (1982), who described the teeth as "slightly bicuspid" or "incipiently bicuspid" (Estes [1965:104] suggested that "the condition is better described as bilobate, as in many Anguidae"). The five anteriormost teeth are not preserved, but the remainder show that the dentary teeth of this lizard are homodont (isodont), without differentiation of tooth form along the tooth row, except that the anterior ones are slightly more slender than those more posterior. Several teeth on the specimen clearly show that deep replacement pits are developed lingually in the tooth bases, implying a direct tooth replacement mode (Edmund, 1969).

Discussion.—The family Xenosauridae is a problematic taxon, and the evolutionary history of the family is poorly known because of its scant fossil record. The North American record of the family includes only three species in two genera: the Oligocene *Exostinus serratus,* the late Paleocene and early Eocene *Restes rugosus,* and the Late Cretaceous *Exostinus lancensis.* These fossil taxa are based mostly on disarticulated materials that are anatomically not comparable between the species. Gauthier (1982) separated *Restes rugosus* from *Exostinus* based on "its unique cephalic osteoderms" and pointed out that *Exostinus lancensis* could well be generically distinguishable from the type species *Exostinus serratus.* On the basis of new evidence revealed from the newly discovered specimens, we offer the following comments on this important but problematic taxon.

The genus *Exostinus* Cope, 1873 (see also Cope, 1884, 1886) includes two species: the type species *E. serratus* (see Cope, 1873) and *E. lancensis* (see Gilmore, 1928). Gauthier (1982) suggested that *E. lancensis* should be removed from *Exostinus* because of the retention of a sulcus dentalis and less extensive intramandibular septum, while Estes (1983*a*) explained the difficulty in taking such a course, owing to the lack of materials that are anatomically comparable between the two species: the type series of *E. serratus* consists of a frontal, a jugal, and a dentary, while a frontal and jugal were unknown for *E. lancensis,* the holotype of which is a maxillary. Now, with the discovery of the frontal (UALVP 29919) and the jugal (UALVP 29920) that are of "*E. lancensis*-type," Gauthier's suggestion seems to be more plausible. The newly recovered frontal shows that the prefrontal incision does not extend to the midpoint of the orbit, and, hence, is significantly different from that of the Oligocene *E. serratus* or that of the Paleocene–Eocene *Restes rugosus.* The jugal and dentary specimens of the Lancian "*E. lancensis*" are also significantly different from the same elements of *E. serratus,* as described above. These differences are apparently great enough to separate the Lancian species from the Oligocene *E. serratus* at a generic level; therefore,

a new generic name should be proposed for the Lancian form. However, it is premature to make such a revision in this paper, before the holotype of the type species *Exostinus serratus* is carefully examined. Therefore, *Exostinus lancensis* is retained in this paper as a valid name.

Estes et al. (1969) referred an unfused frontal (MCZ 3662b) from the Hell Creek Formation to *Exostinus lancensis*. The specimen was not figured, but the description of it raises some uncertainty about this identification: Estes et al. (1969:20) first claimed that "the frontal (MCZ 3662b) may be referable to *E. lancensis* on the basis of dermal sculpture pattern," then stated that the frontal "does not display a sculpture pattern" because it is eroded. With the discovery of new frontal material from the same horizon of definitely *Exostinus lancensis* morphology, the identification of MCZ 3662b is uncertain. In extant xenosaurids, the frontals are fused in the embryo (Estes et al., 1988). This, together with new fossil evidence, indicates that the fused frontal is a primitive character state within the Xenosauridae.

Estes (1964) misspelled *Harpagosaurus* Gilmore, 1928 as "*Marpagosaurus*" in the caption for his plate 5, and later (1983*a*:130) listed "*Marpagosaurus parvus*" as a synonym of Gilmore's *Harpagosaurus parvus* (= *Exostinus lancensis* Gilmore, 1928). In this particular case, Estes' "*Marpagosaurus*" is an "incorrect subsequent spelling" (not an available name), that has no standing in zoological nomenclature, and hence, should not be recorded in synonymy (ICZN, 1985:article 33c).

?*Exostinus* sp.
(Fig. 27G)

Referred Specimen.—UALVP 944, a small but completely co-ossified frontal.

Locality and Horizon.—Outcrop of the Oldman Formation, in Lsd. 10, Sec. 29, Tp. 21, R 12, W 4 (near the Railway Grade locality), southern Alberta; Upper Cretaceous.

Description.—UALVP 944 (Fig. 27G) is the posterior part of a fused frontal, and is the only specimen of this morphology known from the Oldman Formation. Although small, the frontal is so well co-ossified as a single unit that the ventral surface shows no midline suture. The subolfactory processes are broken on both left and right sides, but the broken bases suggest that the processes were ventrally directed and probably not in contact at the midline. In dorsal view, the specimen shows important characters on which its taxonomic assignment is based: it is strongly constricted between the orbits, giving an hourglass shape to the bone; and small tuberculate osteoderms with vermiculate sculpture are fused to its external surface. These osteodermal mounds are all about equal in size and are separated from one another by deep and wide grooves. The specimen is too incomplete to show the prefrontal or postfrontal incision.

Discussion.—UALVP 944 is the first xenosaurid specimen known from the Oldman Formation, which is about 11 Myr older than the Lance and Hell Creek formations (Thomas et al., 1990), from which *Exostinus lancensis* is known. The different osteodermal sculpture clearly distinguishes the Judithian morph from the Lancian *E. lancensis,* and in keeping with the wide geologic gap between the two, is probably taxonomically significant.

The osteodermal sculpture of the Judithian form is structurally more similar to that of the Oligocene *Exostinus serratus* (see Gauthier, 1982:fig. 7) than to either Lancian *E. lancensis* or the Paleocene *Restes rugosus* (see Gauthier, 1982:fig. 5). This condition may suggest that two different lineages are involved in the evolutionary history of the Xenosauridae. However, the fossil record for these taxa is so poor that many taxonomically important characters are unknown as yet. Clarification of their phylogenetic relationships must await discovery of more nearly complete material.

Sahni (1972) reported two xenosaurids from the Judith River Formation by referring AMNH 8497 to "*Exostinus lancensis*" and AMNH 8498 to "cf. *Exostinus* sp." The former specimen, AMNH 8497, is too fragmentary to provide a valid basis for its referral to *Exostinus lancensis,* and seems to be indistinguishable in tooth morphology from AMNH 8491 (Sahni, 1972:fig. 8K), a maxillary that Sahni referred to *Leptochamops denticulatus* (see relevant discussion above). The latter specimen (AMNH 8498) is a left maxillary with the tooth crowns broken off. However, the specimen has cylindrical tooth shafts without a basal expansion (Sahni, 1972: fig. 8F), and is similar in that respect to *Exostinus.* The lateral surface has vermiculate rugosities, but the particular sculpture pattern is somewhat different from that of *E. lancensis* (compare Sahni, 1972: fig. 8E with Estes, 1964:pl. 5). Therefore, it is possible when more nearly complete specimens are found that the Judithian form may prove to be generically different from *Exostinus* (see discussion below).

Genus and species undetermined
(Fig. 27H–J)

Specimens.—UALVP 29914, jugal; UALVP 29915–29918, incomplete maxillaries; and several unnumbered specimens (fragmentary premaxillary, maxillaries, and jugals).

Locality and Horizon.—MR-6 locality, Verdigris Coulee, approximately 30 km east of the village of Milk River, southern Alberta; upper member of the Milk River Formation (Aquilan), Upper Cretaceous.

Description.—UALVP 29914 (Fig. 27H) is an incomplete right jugal with both of its posterodorsal and anteroventral processes broken. The jugal is substantially smaller than UALVP 29920 assigned to *Exostinus lancensis* (see above), but is proportionally compatible with the maxillaries described below from the same locality and horizon. Unlike the Lancian *Exostinus lancensis* and extant xenosaurs, the posterodorsal process of this jugal is narrow, probably the primitive condition. However, the lateral surface is of xenosaurid-type, with vermiculate rugosities on the postorbital branch of the bone. These rugosities are less prominent and arranged in a more random pattern than those in *Exostinus lancensis,* which are concentrated to form tuberculate mounds.

Four maxillaries (UALVP 29915–29918) are tentatively identified as "Xenosauridae, genus and species undetermined," basedon their characteristic osteodermal ornamentation on the lateral surface. UALVP 29915 (Fig. 27I) is the anterior part of a left maxillary, with three broken teeth and vacant spaces for two others. Part of the dorsal process is preserved; the lateral surface is extensively ornamented with vermiculate sculpture. The sculpture is as extensive as, and is similar in pattern to, that of *Exostinus lancensis* (compare with UALVP 29849; Fig. 27A), but the tubercles are less prominent and less concentrated than in that species. Another specimen (UALVP 29918), the anterior part of a right maxillary, shows the same sculpture pattern. As in the Lancian *Exostinus lancensis,* the superior alveolar foramina are small, circular, and equally spaced.

UALVP 29916, 29917 are the posterior parts of maxillaries, both showing a small palatine process associated with a small posterior interior alveolar foramen. The tooth form of this Milk River xenosaurid is best shown in UALVP 29917 (Fig. 27J), which has two complete teeth preserved. The two teeth are posterior to the posterior interior alveolar foramen and probably represent the sixth and fifth positions from the back. The teeth are pleurodont and slightly recurved. The crowns are trenchant, with sharp anterior and posterior blades, but are not serrated. As in other anguimorphans, the tooth bases bear a small medial foramen. The bases are not expanded and also have no infoldings, differing in these respects from those in the Varanoidea.

Discussion.—The specimens described above from the upper member of the Milk River Formation represent an early fossil record for the family Xenosauridae, as the age of the formation has been determined as Aquilan (i.e., early Campanian; see section on geological setting above). The lower taxonomic assignment of this early xenosaurid is difficult, because all the specimens known are fragmentary and other fossil taxa of the same group are still poorly understood (see above discussion). Morphologically, the Milk River jugal (UALVP 29914) is clearly distinguishable from those of the Lancian *Exostinus lancensis* and Oligocene *E. serratus* by its narrow, less heavily sculptured postorbital branch. The sculpture pattern on the lateral surface of the maxillaries (UALVP 29915–29918) closely resembles that on the maxillary that Sahni (1972) described from the Judith River Formation, eastern Montana, but is different from that in the Lancian *E. lancensis.* The resemblance may suggest that the Milk River and Judith River materials are congeneric; however, a reliable taxonomic assignment of these fossils must await the discovery of better preserved specimens.

Finally, it must be pointed out that there is no direct evidence for the association of the Milk River jugal with the maxillaries discussed above. These materials are tentatively placed together, leaving only one xenosaurid lizard recognized from the Milk River Formation. However, further study on more extensive materials could well change this association.

Family Anguidae Gray, 1825

The family Anguidae includes the so-called glass lizards, alligator lizards, and related species. Most members of the family are heavily scaled or armour-plated, and have a lateral fold of body squamation (McDowell and Bogert, 1954) "which allows for distention of their otherwise inflexible skin when they are carrying eggs or have eaten a large meal" (Mattison, 1989:167). A strong tendency within the family is towards limb reduction or loss, and some are snake-like in the complete loss of limbs (for other recognized synapomorphies, see Estes et al., 1988). The Anguidae contain some 80 extant species, and have a geographical distribution in North and South America and the West Indies, and in Europe, central, south, and southeast Asia, and northwesternmost Africa. All species are carnivorous, and their prey includes insects, small mammals, other lizards, and molluscs. The family has its best fossil record from North America and Europe (see Estes, 1983*a*:fig. 65).

Genus *Odaxosaurus* Gilmore, 1928

Type Species.—Peltosaurus? piger Gilmore, 1928.

Range.—Upper Cretaceous, North America. Several Paleocene and Oligocene specimens were previously referred to *Odaxosaurus,* but lately have been placed in *Proxestops* Gauthier, 1982, or *Machaerosaurus* Gilmore, 1928 (see discussion below). Accordingly, the geologic range of *Odaxosaurus* may not extend to the Paleocene; for pre-Lancian *Odaxosaurus,* see later discussion.

Diagnosis (after Estes, 1983a:147).—"Differs from other glyptosaurine lizards in having paired

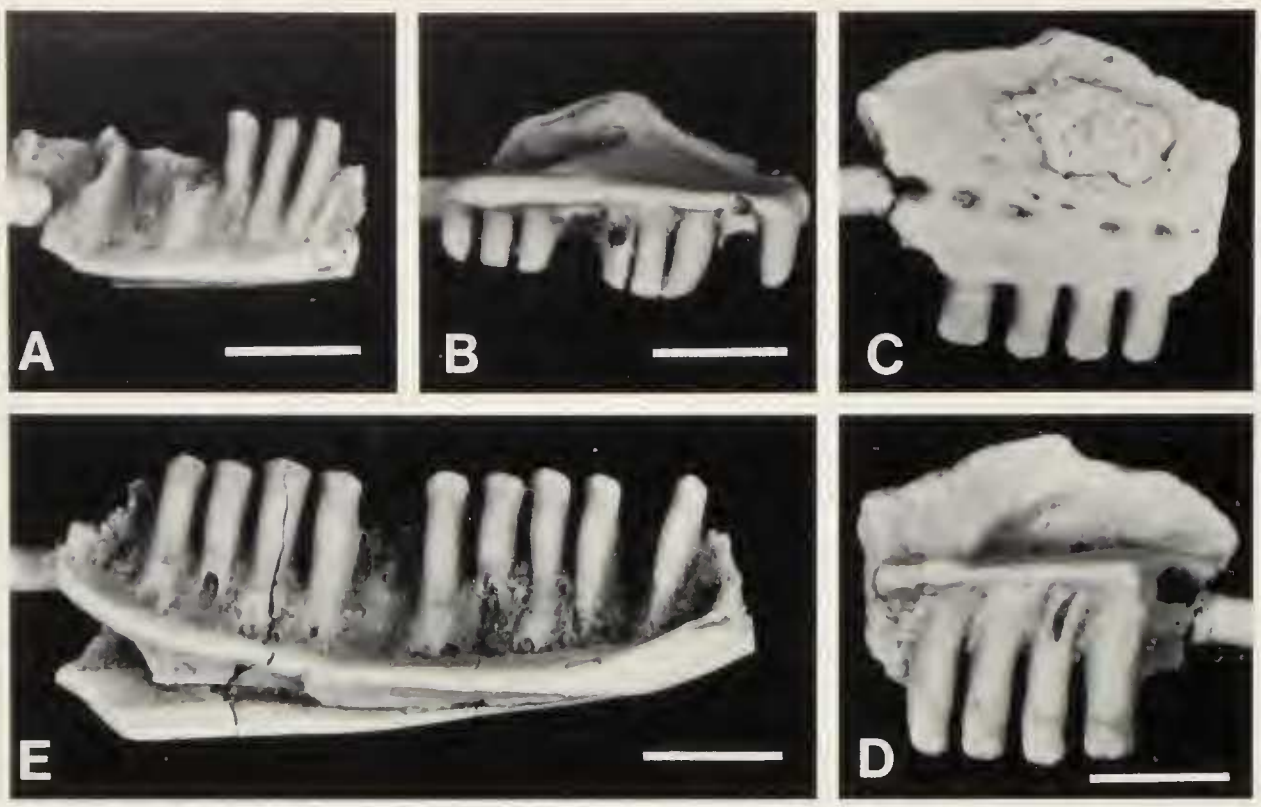

Fig. 28.—*Odaxosaurus piger,* Scollard (Alberta), Frenchman (Saskatchewan) and Lance (Wyoming) formations: A, UALVP 33381, incomplete left dentary, medial view; B, UALVP 33382, incomplete left maxillary, medial view; C, D, UALVP 29851, incomplete right maxillary, lateral and medial views; E, UALVP 29852, nearly complete left dentary, medial view. Scale = 2 mm.

frontals (which may fuse in Paleocene individuals if correctly referred); vermiculate (nontubercular) osteodermal sculpture; rectangular osteoderms with poorly developed lateral bevels; teeth obtuse, shafts expanded transversely, crowns squared off with an anteroposteriorly oriented but slightly oblique cutting edge striated lingually and labially" (but see discussion below).

Odaxosaurus piger (Gilmore, 1928) (Fig. 28)

Peltosaurus? piger Gilmore, 1928:136, pl. 26, fig. 4, 6.
Odaxosaurus obliquus Gilmore, 1928:158, pl. 26, fig. 3, 5.
Peltosaurus piger Estes, 1964:119.
Pancelosaurus piger Meszoely, 1970:105.

Holotype.—USNM 10687, incomplete right dentary with six teeth. Collected by O. A. Peterson in 1889, from "Peterson's quarry," Lance Creek, Niobrara County, Wyoming (Gilmore, 1928).

Referred Specimens.—Scollard Formation, KUA-3 locality: UALVP 33381, dentary; Frenchman Formation, Wounded Knee locality: UALVP 33382, maxillary.

Known Distribution.—Upper Cretaceous Lance Formation, eastern Wyoming; Hell Creek Formation, eastern Montana; Laramie Formation, Colorado (Carpenter, 1979); Scollard Formation, central Alberta; and Frenchman Formation, southwestern Saskatchewan (all Lancian). Some specimens of Judithian and Paleocene age have been referred to this species, but none of the referrals are convincing (see later discussion).

Diagnosis.—A Lancian *Odaxosaurus* differing from the new species described below in the following combination of character states: dentary teeth crowded along tooth row; tooth crowns strongly truncate, heavily striated both medially and laterally; tooth shafts strongly expanded transversely, with well-developed medial shoulder-like expansion, rectangular in cross section; intramandibular septum short, deep, not extending anteriorly to midpoint of tooth row.

Description.—UALVP 33381 (Fig. 28A) from the KUA-3 locality (Scollard Formation) is an incomplete left dentary with seven tooth positions preserved (three teeth and broken bases as well as vacant spaces for four others). This specimen is referred to *Odaxosaurus piger* as it shows the same tooth form and dentary structure as the type Lance specimens (see Gilmore, 1928; Estes, 1964). As in the Lance specimens, this dentary bears pleurodont teeth, which have subrectangular bases, anteroposteriorly compressed and medially expanded shafts, and chisel-shaped crowns with a horizontal cutting edge and vertical striations. These are the diagnostic characters for *Odaxosaurus piger* (Gilmore, 1928; Estes, 1964). The dentary is broken posteriorly at the anterior inferior alveolar foramen, and hence, the notch for the foramen on the tooth-bearing border is not preserved, nor is the intramandibular septum posteriorly within the Meckelian canal.

UALVP 33382 (Fig. 28B) from the Wounded Knee locality (Frenchman Formation) is a left maxillary with nine tooth positions (seven teeth and broken bases for two others). The referral of this maxillary to *Odaxosaurus piger* is principally on a large

posterior interior alveolar foramen that is associated with a large palatine process. These characters are distinct for *Odaxosaurus,* and are different from gerrhonotines, which have a much smaller or no palatine process and have two posterior interior alveolar foramina (Meszoely, 1970; personal observation). As a result of erosion, the tooth crowns show no horizontal cutting edge and vertical striations, but enough remains to show that the teeth are squared off and laterally compressed. The tooth bases are like those of specimens from the Lance, subrectangular in shape and bearing a small basal foramen.

In addition to the specimens described above, some 13 maxillaries and 27 dentaries from the Lance and Hell Creek formations are included in this study because these specimens provide new information for a better understanding of *Odaxosaurus piger,* and provide comparative materials for the study of the Scollard and Frenchman specimens. The Lance specimens were collected from the BTB locality, and include one maxillary (UALVP 29851) and five dentaries (UALVP 29852–29856). The Hell Creek specimens were from the BCA locality, and include 12 maxillaries (UALVP 29857–29861, 29879–29885) and 22 well-preserved dentaries (UALVP 29862–29878, 29886–29890).

UALVP 29851 (Fig. 28C, D) is an incomplete right maxillary having four teeth preserved. Although fragmentary, the specimen is of importance as it shows unworn tooth crowns and osteoderms on its lateral surface. The marginal teeth of this lizard have the characteristic combination of a chisel-shaped lateral cutting edge (previously known) and a remnant medial cusp (unknown before). A well-preserved dentary (UALVP 29852, see below) shows the same crown pattern, while most of the other specimens have no medial cusp as the result of wear. The tooth crowns are striated both lingually and labially, but the lingual striations are obviously stronger than those on the labial side. An osteoderm is fused to the lateral surface of the maxillary (a similar structure is seen on UALVP 29887, a dentary from the BCA locality). The osteoderm is thick and tuberculate, and is different from those on the previously referred parietals and frontals (see Estes, 1964, 1983*a*), which are thin plates with a gerrhonotine–diploglossine type of sculpture (Estes, 1964; Meszoely, 1970).

The crown pattern of the dentary teeth is best shown on UALVP 29852 (Fig. 28E), an incomplete left dentary having nine teeth and the spaces for four others. As in the maxillary described above, the teeth of this specimen show a combination of a chisel-like lateral cutting edge with a remnant medial cusp. However, this crown pattern varies along the tooth row: the slightly procumbent anterior teeth have a less well-developed cutting edge but a stronger medial cusp, while the posterior teeth, which are shorter than the anterior ones, have a stronger cutting edge and a weaker medial cusp. The Meckelian canal is anteriorly restricted to form a shallow and ventrally facing groove, but gradually turns more ventromedially in the posterior half of the dentary. The ventral edge of the strongly reduced subdental shelf bears a lateral extension in front of the anterior inferior alveolar foramen, forming a flat surface for attachment of the splenial.

Discussion.—Odaxosaurus piger has a complex taxonomic history, one in which its taxonomic name has been changed several times. Gilmore (1928:136, 158) named *Peltosaurus*? *piger* and *Odaxosaurus obliquus* based on several specimens from the Lance Formation, eastern Wyoming. Estes (1964) synonymized *Odaxosaurus obliquus* with *Peltosaurus*? *piger,* and firmly referred the species to *Peltosaurus* Cope, 1872; meanwhile, he also provided solid evidence for the familial assignment of *Peltosaurus piger* to the Anguidae from the construction of the dentary. More recently, Meszoely (1970) removed the species from *Peltosaurus* based on differences in jaw and osteodermal sculpture, and named a new genus, *Pancelosaurus,* for *Peltosaurus piger.* Meszoely et al. (1978) published the most recent revision of the genus, and finally clarified the taxonomic status of this species. They reviewed all of the nomenclatural controversy, restudied the holotype of *Odaxosaurus obliquus,* and came to the following conclusions: 1) Gilmore's *Odaxosaurus obliquus* is indistinguishable from *Peltosaurus*? *piger*; 2) Gilmore's *Peltosaurus*? *piger* is generically different from *Peltosaurus,* and should be removed from the genus; 3) *Pancelosaurus* Meszoely, 1970, is a synonym of *Odaxosaurus* Gilmore, 1928; and 4) according to ICZN rules, both the generic name "*Odaxosaurus*" and specific epithet "*piger*" have priority; thus, the proper name for this lizard is *Odaxosaurus piger.*

Gilmore (1928) classified *Odaxosaurus piger* (his "*Peltosaurus*? *piger*") in the Anguidae, and first noticed its similarity in tooth morphology to *Glyptosaurus* Marsh, 1871. This familial placement was questioned by McDowell and Bogert (1954), but has been solidly confirmed by Estes (1964) on the basis of dentary structure. However, the taxonomic status of *Odaxosaurus piger* at the subfamilial level is still in dispute. The family Anguidae is commonly subdivided into four subfamilies: Anguinae, Glyptosaurinae, Gerrhonotinae, and Diploglossinae (see, e.g., McDowell and Bogert, 1954; Meszoely, 1970; see also Estes, 1983*a,* for a different classification). Meszoely (1970) recognized the basal position of *Odaxosaurus* in anguid phylogeny, and referred it to the subfamily Anguinae on the basis of its *Ophisaurus*-like osteoderms. Sullivan (1982) proposed a subfamilial name Odaxosaurinae for *Odaxosaurus piger,* separating this species from Glyptosaurinae on the basis of its nontubercular osteoderms (but see description above). This idea is further developed in his later publications (see Sullivan, 1986*a,* 1986*b*). After careful evaluation of the character states of this lizard, Estes (1983*a*) put greater weight on tooth morphology than sculpture pattern of the osteoderms, and classified *O. piger* in the Glyptosaurinae, as its most primitive member (Estes, 1983*a*:148).

The evidence that Sullivan (1982, 1986*a,* 1986*b*) used to separate *Odaxosaurus* from the Glyptosaurinae as a subfamily is quite problematic: first, the

holotype of *Odaxosaurus piger* is a dentary with teeth, not a skull element with osteoderms; thus, characters of tooth morphology and dentary structures must be relied on for interpreting the relationships of this lizard. Second, the referral of those parietals and frontals having nontuberculated sculpture to *Odaxosaurus piger* is questionable, as two jaw specimens (UALVP 29851, 29887) show osteodermal sculpture different from those on the referred parietals and frontals (thick tuberculate mounds vs. thin plates with a vermiculate sculpture). The referral of the Lance disarticulated parietals and frontals to *O. piger* is based mainly on size and relative abundance of individuals (see Meszoely, 1970:105). Estes (1964:122) pointed out that "the pitted and ridged sculpture pattern of these osteoderms resembles most Recent *Gerrhonotus.*" Meszoely (1970:108) correctly noted that: "the frontals of *Odaxosaurus piger* resemble closely those of Recent *Diploglossus*; they agree in general outline. . .and in having nearly identical sculpture on the osteoscutes covering these bones." However, Estes (1983*a*) saw that the species has a derived, glyptosaurine-like tooth form. Here, we have a Cretaceous anguid lizard with glyptosaurine tooth morphology and jaw structure but diploglossine skull elements and osteoderms, with association with the skull elements based on size and relative abundance of the fossils. Therefore, the question is whether this referral is correct or the skull elements actually represent an anguid lizard other than *Odaxosaurus.* In fact, Armstrong-Ziegler (1980:21) had already questioned this referral by stating that "the dentaries of both *Gerrhonotus* and *Pancelosaurus* occur in the Lance Formation; Meszoely (1970, p. 105) assigned the above defined osteoscutes to *Pancelosaurus* instead of *Gerrhonotus* on the basis of the greater abundance of skull remains of *Pancelosaurus* relative to *Gerrhonotus.* This criterion of relative abundance used by Meszoely does not seem sufficient reason to assign these osteoscutes to *Pancelosaurus* or *Gerrhonotus.*" The discovery of the jaw materials with fused osteoderms (see description above) implies more strongly than before that the association of these disarticulated materials is incorrect.

It appears that the early history of Anguidae involved two major evolutionary lines: the diploglossine (gerrhonotine) line and the glyptosaurine line. The former includes those anguids that are essentially predatory, with sharp teeth and relatively thin, nontuberculated osteoderms; and the latter line includes those nonpredatory anguids having blunt teeth with a thick enamel cap for a durophagous diet, and a heavy armor of thick, tuberculated osteoderms. From jaw structure and tooth form, *Odaxosaurus piger* is obviously on the glyptosaurine line; and the skull elements previously referred to *O. piger* are possibly associated with some kind of predatory anguid, as the osteodermal sculpture on these bones is closely similar to the *Diploglossus–Ophisaurus* type (Estes, 1964; Meszoely, 1970). This type of osteoderm is also known from the Oligocene *Parophisaurus* Sullivan, 1987, the anguid lizard that is ideal as the structural ancestor of *Ophisaurus* (Sullivan, 1987).

Odaxosaurus piger is known only from Lancian horizons, including the Lance, Hell Creek, Laramie, Scollard, and Frenchman formations. Several Paleocene and Oligocene specimens were previously referred to this species (Meszoely, 1970; Estes, 1975, 1976; Sullivan, 1979, 1981, 1982), but have recently been reassigned to *Proxestops silberlingi* or *Machaerosaurus* (Gauthier, 1982; Estes, 1983*a*; Sullivan, 1986*b,* 1991); therefore, no definite *Odaxosaurus piger* specimen is known from post-Lancian horizons. Pre-Lancian *Odaxosaurus* lizards were previously reported from the Judith River Formation (Sahni, 1972), Mesaverde Formation (see Estes, 1983*a*), and Oldman Formation (Fox, 1976). Our study of the specimens from the Oldman Formation reveals that the Judithian *Odaxosaurus* represents another species different from Lancian *O. piger.*

Odaxosaurus priscus, **new species**
(Fig. 29, 30A–F)

Etymology.–Priscus (Latin), meaning "former, aboriginal."

Holotype.—UALVP 29896, incomplete right dentary with eight teeth and spaces for six others.

Type Locality and Horizon.—Outcrop of the Oldman Formation near Irvine, in Sec. 31, Tp. 11, R 2, W 4, about 40 km east of Medicine Hat, southeastern Alberta; Upper Cretaceous Oldman Formation (Judithian).

Referred Specimens.—Railway Grade locality: UALVP 29891, maxillary. Irvine locality: UALVP 29892, 29893–29895, maxillaries; UALVP 29897–29902, 33380, dentaries.

Known Distribution.—Type Irvine and Railway Grade localities, Oldman Formation (Judithian), southeastern Alberta.

Diagnosis.—A Judithian *Odaxosaurus* differing from the Lancian *O. piger* in the following combination of character states: dentary teeth fewer, further apart from each other; tooth crowns less trun-

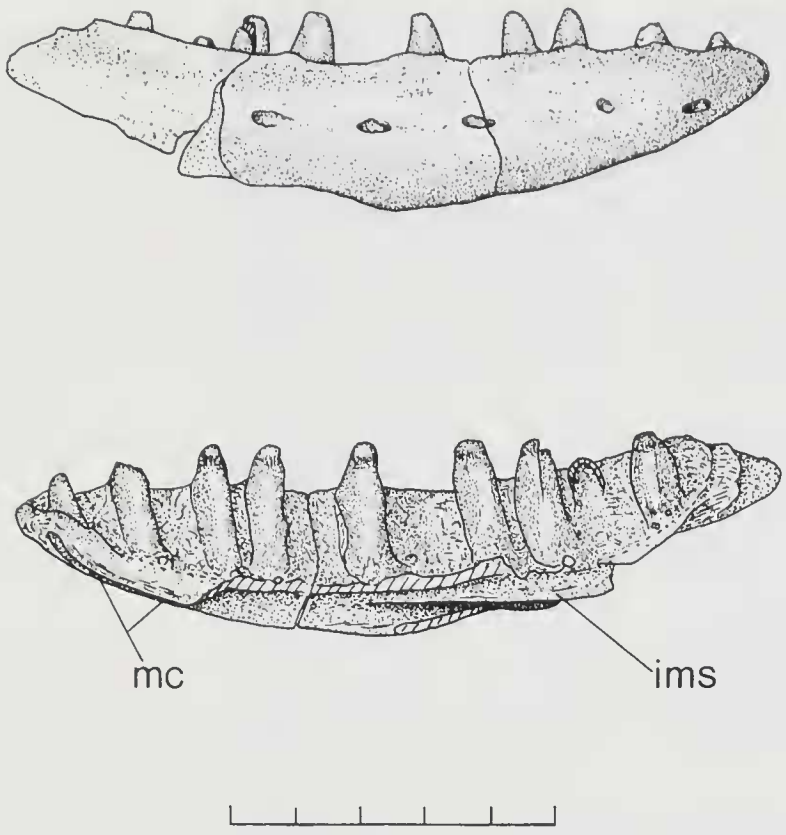

Fig. 29.—*Odaxosaurus priscus,* new species, Oldman Formation, Alberta: UALVP 29896 (holotype), incomplete right dentary, lateral (above) and medial (below) views. Scale = 5 mm. Abbreviations as in Fig. 2.

cate, less flaring anteriorly and posteriorly in side view, and less heavily striated medially; intramandibular septum not so strongly developed, with free ventral border extending further anteriorly, to midpoint of tooth row.

Description.—The holotype, UALVP 29896 (Fig. 29, 30A), is a right dentary showing that the jaw configuration of this lizard is similar to that of the Lancian *Odaxosaurus piger.* This specimen retains a complete tooth row, with eight teeth and the spaces for six others, giving a total of 14 positions. As in *O. piger,* the tooth shafts are strongly compressed anteroposteriorly and have a strong, shoulder-like, medial expansion. The tooth crowns on this specimen are partially dissolved, but are apparently less truncated than those in *Odaxosaurus piger,* especially for the anterior and middle teeth. These teeth are also more widely spaced than in *Odaxosaurus piger.*

Medially, most of the subdental shelf has been broken away; thus, the notch for the anterior inferior alveolar foramen is not shown on this specimen. However, four other dentaries (UALVP 29897–29898, 29900, 29902) clearly show that the notch forms the dorsal and anterior border of the anterior inferior alveolar foramen. The Meckelian canal is as ventrally restricted as in *O. piger,* but the intramandibular septum is significantly shallower and less vertically directed compared to the latter species, and has a free ventral border extending anteriorly to the midpoint of the tooth row.

Another dentary, UALVP 29897 (Fig. 30B), has seven teeth and the bases for four others preserved. The crowns of most of the teeth are badly worn, but one posterior tooth (probably the fourth from the back) clearly shows that the crown is chisel-shaped. The sulcus dentalis is entirely lacking, and the subdental shelf is greatly reduced to form a smooth, sloping border with a small notch for the anterior inferior alveolar foramen. Like the holotype, this dentary also shows that the free ventral border of the intramandibular septum extends anteriorly beyond the anterior inferior alveolar foramen to the midpoint of the tooth row, differing in that respect from *Odaxosaurus piger,* in which the septum extends only to the point below the foramen.

The dentary teeth are best shown on UALVP 33380 (Fig. 30C), a specimen from the Irvine locality. On this specimen, two well-preserved posterior teeth above the intramandibular septum show that the tooth shafts, like those of *Odaxosaurus piger,* are anteroposteriorly compressed and have a shoulder-like medial expansion. However, unlike the posterior teeth in *O. piger,* the two teeth have slightly recurved crowns with faint medial striations (but lack lateral striations). Well-preserved posterior teeth on UALVP 29894, a maxillary, consistently show the same type of crown pattern (see later description).

Among the five maxillaries referred to this species, two are obviously better preserved than the others. UALVP 29891 (Fig. 30D) from the Railway Grade locality is from the right side and bears four teeth and the bases as well as spaces for seven others. The specimen shows essentially the same configuration as that of Lancian *Odaxosaurus piger,* but has a much more prominent premaxillary process. The posterior interior alveolar foramen is single, large, and located above the ninth or tenth tooth position from the front. Unlike the maxillary in the Lancian species, however, this specimen shows that the crowns of the anterior and middle teeth are bluntly unicuspid, slightly recurved, but clearly show a tendency towards development of a lateral cutting edge. In occlusal view, the tooth crowns have a central cusp that curves lingually and posteriorly, forming an "inwardly pointing V" (see Estes, 1964). The medial striations on these teeth are much weaker than in *O. piger* and the lateral surfaces show no striations at all. The posterior teeth of UALVP 29891 are not preserved, but must have had chisel-shaped crowns, as clearly shown on the dentary specimens.

Another maxillary, UALVP 29892, is from the left side and has five teeth and the bases for four others. Like UALVP 29891, this specimen also shows a prominent premaxillary process (see Fig. 30E). The lateral parapet of the maxillary is broken immediately behind the ninth tooth position, but it still clearly shows that a single and large posterior interior alveolar foramen is located above the tenth tooth position. The tooth crowns on this specimen are not well preserved, but are similar in shape to those of UALVP 29891.

The other three specimens (UALVP 29893–29895) are less well preserved than the two described above, in terms of showing the general shape of the maxillary. However, these are significant, because the teeth on these specimens show slightly recurved crowns with faint medial, but no lateral striations, consistent with the posterior dentary teeth described above. UALVP 29894 (Fig. 30F) has badly worn tooth crowns, indicating it is from an old individual, while UALVP 29895 shows a prominent palatine process closely associated with a single large posterior interior alveolar foramen, as in Lancian *O. piger.*

Discussion.—The holotype described above from the Oldman Formation represents a new, Judithian species of *Odaxosaurus,* which differs principally from the Lancian *O. piger* in having fewer, less truncate dentary teeth, and a shallower intramandibular septum extending anteriorly to the midpoint

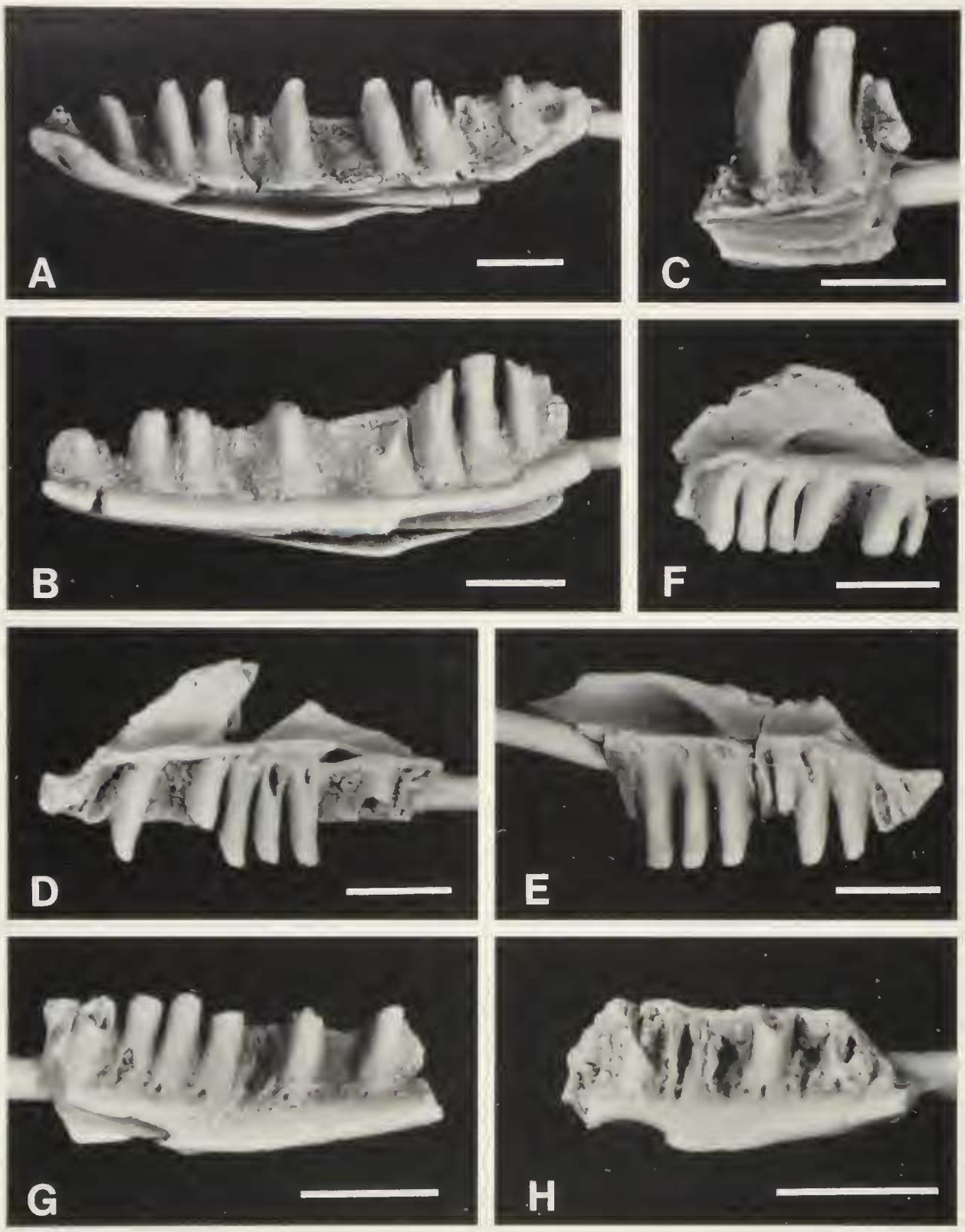

Fig. 30.—*Odaxosaurus priscus*, new species, Oldman Formation, Alberta: A, UALVP 29896 (holotype), incomplete right dentary, medial view; B, UALVP 29897, incomplete right dentary, medial view; C, UALVP 33380, right dentary fragment, medial view; D, UALVP 29891, right maxillary, medial view; E, UALVP 29892, left maxillary, medial view; F, UALVP 29894, right maxillary, medial view. Anguidae, genus and species undetermined, Milk River Formation, Alberta: G, UALVP 33378, incomplete left dentary, medial view; H, UALVP 33379, fragmentary left dentary, medial view. Scale = 2 mm.

of the tooth row. Referred specimens from the same formation show other taxonomically significant character states for the new species, including the possession of a more prominent premaxillary process of the maxillary and tooth crowns having much weaker medial striations (while no lateral striations are shown on these specimens). *Odaxosaurus priscus* is clearly on the glyptosaurine line of evolution, as evidenced by its close resemblance in dentary structure and tooth morphology to the Lancian *O. piger*, which is currently regarded as a precusor of the Tertiary true glyptosaurines (Estes, 1983*a*; Sullivan, 1986*a*, 1986*b*). The dentary of this Judithian form has a shallow but anteriorly extending intramandibular septum, and obtuse teeth with faint medial striations, from which the Lancian *O. piger* can

easily be derived. Therefore, the Judithian species represents the earliest known stage in glyptosaurine evolution. There are no osteoderms directly associated with *O. priscus* (e.g., fused to the maxillary or dentary specimens), but its characteristic tooth morphology and dentary structure indicate that the splitting of glyptosaurines from their ancestral group can be traced at least back to Judithian time.

Several authors have referred specimens of Judithian age to the Lancian species *Odaxosaurus piger,* but this study shows that these referrals are either erroneous or unconvincing: Sahni (1972:354) referred two specimens (AMNH 8494, 8495) from the Judith River Formation to "*Peltosaurus piger*" (= *Odaxosaurus piger*) based on the characters that are symplesiomorphic for the family Anguidae (e.g., "anteriorly the Meckelian fossa is ventral in position"). Regarding Sahni's referral of these two specimens to *Odaxosaurus piger,* we here offer the following comments: 1) AMNH 8494 (Sahni, 1972: fig. 8H), an incomplete right dentary with all of the teeth broken off, is certainly an anguid as it shows a notch on a greatly reduced subdental shelf in combination with the loss of the sulcus dentalis. However, it differs from the dentary of *Odaxosaurus* in having a straight tooth-bearing border, and more importantly, having cylindrical but not transversely expanded tooth shafts (personal observation). Similar materials are also known from the Oldman and Milk River formations, which are identified as "Anguidae, genus and species undetermined" in this paper. 2) AMNH 8495 (Sahni, 1972:fig. 8G) as described appears to be referrable to *Odaxosaurus,* as Sahni (1972:354) stated that "the teeth are pleurodont, linguolabially expanded, and the transverse width is only slightly smaller than the height. The crown is expanded relative to the shaft and consists of a distinct anteroposteriorly directed crest rather than separate cuspules." However, the clear figure of the specimen (Sahni, 1972:fig. 8G) contradicts this description, and indicates that it is largely artificial. In fact, all but one tooth on the maxillary are broken off, and the one preserved is slender, definitely neither chisel-shaped nor striated (personal observation). A large resorption pit of this tooth is also substantially different from the small, rounded basal foramen in *Odaxosaurus.* Therefore, this specimen should be excluded from *Odaxosaurus.* The specimen is more or less *Contogenys*-like, but its fragmentary nature does not allow a familial referral. Although AMNH 8494, 8495 may not pertain to *Odaxosaurus,* some of the maxillary and dentary fragments in a specimen box (labelled as AMNH 8496) are indeed of the *Odaxosaurus* kind, indicating occurrence of this genus in the Judith River Formation.

Estes (1983*a*) referred several specimens from the "Mesaverde" Formation in Wyoming to the species *Odaxosaurus piger* in his monographic review of fossil lizards. Without a description or figure, it is difficult to evaluate the reliability of this identification.

Genus and species undetermined (Fig. 30G, H)

Referred Specimens.—Milk River Formation, MR-4 locality: UALVP 33378, incomplete left dentary. MR-6 locality: UALVP 33379, fragmentary left dentary. Many unnumbered maxillary and dentary fragments from MR-4, MR-6, MR-8, and MR-20 localities.

Description.—UALVP 33378 (Fig. 30G) consists of the middle and posterior part of a small left dentary, bearing six teeth and vacant positions for two others. The lateral surface of the dentary is smooth, lacking any sculpture. Three inferior alveolar foramina preserved on the specimen are large, open anterolaterally, and aligned horizontally about midway in the height of the dentary. These foramina are more or less equally spaced from one another. Medially, the subdental shelf is greatly reduced as a smoothly sloped tooth-bearing border, which is posteriorly notched for the anterior inferior alveolar foramen. The Meckelian canal anterior to the notch cannot be seen in medial view; however, a ventral view shows that the canal is greatly restricted, opening ventrally throughout most of its length as a shallow and narrow gutter. A slightly flattened ventral surface of the dentary anterior to the notch indicates that a greatly reduced splenial terminated anteriorly close to the midpoint of the tooth row. Posteriorly within the Meckelian canal, a clearly defined intramandibular septum is vertically directed; it has a free ventral border and is posteriorly notched for the Meckelian cartilage.

The dentary teeth are high-crowned, having a cylindrical shaft and a small basal foramen opening medially at the tooth base. Most of the teeth have the crowns broken off, but two are well preserved and show that the crowns have faint medial striations. These teeth are pleurodont, having two-thirds of their height attached to the well-developed lateral parapet of the dentary. A more fragmentary dentary of this kind (UALVP 33379; Fig. 30H) is known from the MR-6 locality. It has the same jaw construction and proportions as the above-described specimen; the size, notched tooth-bearing border, and well-developed intramandibular septum match UALVP 33378 and allow both to be referred to the same species. On the basis of similar jaw construction and proportions, several unnumbered maxillary and dentary fragments from the Milk River Formation are also referrable to Anguidae, genus and species undetermined. These specimens were collected from MR-4, MR-6, MR-8, and MR-20 localities.

Discussion.—Fox (1972*a*, in schedula) made the original identification of the above-described specimens as anguids. As a result of this study, the placement of these specimens in the Anguidae is supported by a well-recognized synapomorphy: the strongly reduced subdental shelf is notched for the

anterior inferior alveolar foramen, so that the dentary forms the dorsal and anterior border of the foramen (Estes, 1964; Estes et al., 1988). Two other character states shown on these specimens are synapomorphic for a higher taxon, Anguimorpha; these include: a Meckelian canal that opens ventrally anterior to the anterior inferior alveolar foramen, and a posterior part of the Meckelian canal that is subdivided by a ventrally directed intramandibular septum (Estes, 1964; Estes et al., 1988). These specimens also show a great reduction of the subdental shelf corresponding with the total loss of the sulcus dentalis, as is commonly seen in other anguimorphans.

Although undetermined at generic and specific levels, the identification of these specimens as Anguidae (Fox, 1972*a*, in schedula) is significant, as these early Campanian materials document the earliest undoubtedly fossil record for this family. Previous to the present study, Winkler et al. (1990) reported "Anguidae?" from the Comanchean Paluxy Formation, central Texas. However, the specimen figured (SMU 72297; see Winkler et al., 1990: fig. 8E) has a robust subdental shelf and a sulcus dentalis, suggesting a scincomorphan affiliation, rather than anguid. Therefore, the Comanchean specimen should be excluded from the Anguidae, making the Milk River specimens described above represent the earliest known record of the family.

Family Necrosauridae* Hoffstetter, 1943

The Necrosauridae* are primitive varanoids characterized by having an unretracted naris, and lacking a ventral contact of the subolfactory processes of the frontal (Estes, 1983*a*). The extinct family includes fossil taxa such as: *Necrosaurus* Filhol, 1876, and *Eosaniwa* Haubold, 1977, from the Tertiary of Europe; and *Parasaniwa* Gilmore, 1928, *Colpodontosaurus* Estes, 1964, (Late Cretaceous), and *Provaranosaurus* Gilmore, 1942, (Paleocene) from North America. The family may also include several Cretaceous forms known from the Gobi Desert (Borsuk-Bialynicka, 1984), but the phylogenetic relationships of the Gobi taxa need further study. The family Necrosauridae* is cladistically treated as a metataxon (Estes et al., 1988), as neither its monophyly nor positive paraphyly can be recognized at present.

Genus *Colpodontosaurus* Estes, 1964

Type Species.—*Colpodontosaurus cracens* Estes, 1964.

Range.—Upper Cretaceous, North America.

Diagnosis.—As for the type and only known species.

Colpodontosaurus cracens Estes, 1964 (Fig. 31A–C)

Holotype.—UCMP 46608, an incomplete left dentary having broken bases for three, and vacant spaces for 12, dentary teeth. The holotype was figured by Estes (1964:fig. 60) with several teeth restored from other specimens.

Referred Specimens.—Scollard Formation, KUA-3 locality: UALVP 33388, fragmentary left dentary. In addition, some specimens from outside the study area are also included in this paper, because they show significant individual variation within the species. These specimens include: Lance Formation, BTB locality: UALVP 29781–29784, incomplete dentaries. Hell Creek Formation, BCA locality: UALVP 29785, 29786, fragmentary dentaries.

Known Distribution.—Upper Cretaceous Lance Formation, eastern Wyoming; Hell Creek Formation, eastern Montana; and Scollard Formation, central Alberta, (all Lancian).

Diagnosis (Revised from Estes, 1983a).—A Late Cretaceous necrosaurid lizard differing from *Provaranosaurus* Gilmore, 1942*a*, its closest known relative, in having: dentary more slenderly built; marginal teeth lower crowned; tooth bases expanded, lacking striations; and having a distinct small ventral process on the weakly developed intramandibular septum, which lacks a free ventral border.

Description.—UALVP 33388 (Fig. 31A) is the only specimen of this species collected from the Scollard Formation. The fragmentary left dentary bears a broken tooth and the vacant spaces for three others. Like the specimens from the Lance and Hell Creek formations, this dentary shows taxonomically significant features: the subdental shelf (without sulcus dentalis) is in a very low position; the tooth base is expanded, lacks striations, and has a basal foramen opening posteromedially; the teeth are hollow and have strongly constricted and possibly recurved crowns (comparing UALVP 33388 with UALVP 29782; see Fig. 31). The size and robustness of this dentary compared with those from the Lance and Hell Creek formations indicate that the Scollard specimen is probably from a relatively old individual.

Among the several specimens of *Colpodontosaurus cracens* from the BTB locality in the UALVP collections, UALVP 29781 (Fig. 31B) is relatively complete, with only the anterior end missing. The dentary shows the same general configuration as the holotype of the species, but differs from the latter in having four (rather than two) inferior alveolar foramina on its lateral surface, although it is smaller than the holotype. There are no teeth preserved on the specimen, but spaces for 13 tooth positions can be clearly recognized. The total number of dentary teeth for this lizard is estimated at close to 20, as in the holotype.

Another specimen (UALVP 29782; Fig. 31C) is the posterior part of a right dentary, including the posteriormost eight tooth positions. This dentary has three incomplete teeth preserved, showing that the tooth bases are expanded, nonstriated, and each

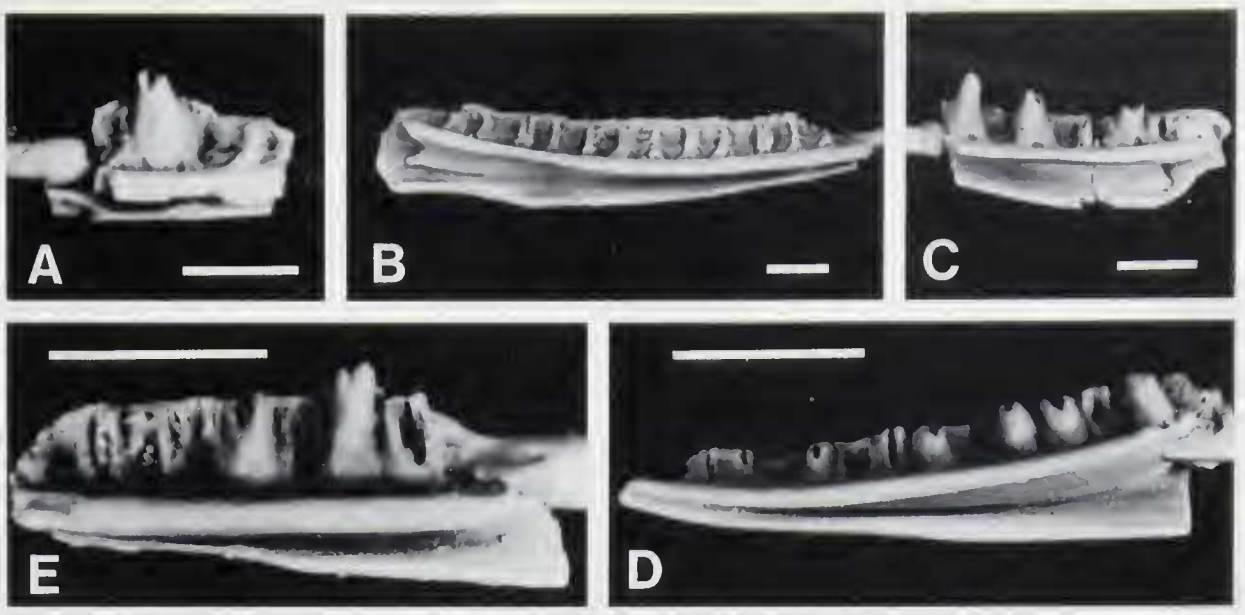

Fig. 31.—*Colpodontosaurus cracens*, Scollard and Lance formations, Alberta and Wyoming: A, UALVP 33388, left dentary fragment, medial view; B, UALVP 29781, left dentary, medial view; C, UALVP 29782, right dentary fragment, medial view. Necrosauridae*, new genus and species (unnamed), Milk River Formation, Alberta: D, UALVP 29787, incomplete right dentary, medial view; E, UALVP 33383, incomplete right dentary, medial view. Scale = 2 mm.

bears a small foramen. The tooth crowns are strongly constricted, and are obviously less recurved than those Estes (1964) figured for the holotype. The intramandibular septum is similar to that of the holotype and the other specimens included in this collection, in lacking a free ventral border but having a tiny ventral process.

Discussion.—The Lancian *Colpodontosaurus cracens* was originally diagnosed by Estes (1964) as a lizard having thin-walled, pointed, recurved, and short teeth; and having a tiny free ventral process of the intramandibular septum. The specimens in the UALVP collections from the Lance and Hell Creek formations provide no new information relevant to the diagnosis of this lizard, but show some variation in the curvature of the dentary teeth and the number of inferior alveolar foramina. Estes (1964:fig. 60) figured the holotype with strongly recurved teeth (restored from other specimens, according to Estes), while UALVP 29782 shows that the teeth have a relatively straight shaft with only the tip of the crown slightly recurved. The holotype, as Estes (1964) described, has only two inferior alveolar foramina on its lateral surface, while UALVP 29781 (also UALVP 29785) shows four foramina. Recognition of these variations is significant for a better understanding of this poorly known species.

Estes (1964) originally placed *Colpodontosaurus cracens* in the Diploglossa (Anguioidea) incertae sedis, on the basis of the tiny ventral process of the intramandibular septum, absence of basal infoldings of the teeth, and the presumed lack of an intramandibular hinge. More recently, Estes (1983*a*), referred this species to the Necrosauridae* on the basis of resemblances in jaw and tooth structure to some necrosaurids (e.g., lack a free ventral border of the intramandibular septum as in necrosaurids generally; thin-walled teeth as in *Provaranosaurus*). This familial placement is followed in this paper. However, *Colpodontosaurus cracens* is based on dentary materials (in most cases on specimens with the teeth broken off), and maxillary and other skull elements are unknown or poorly known as yet. A better understanding of the relationships of this lizard at and below the familial level depends on further study of better preserved materials.

Genus and species new (unnamed)
(Fig. 31D, E)

Referred Specimens.—UALVP 29787, 33383; both right dentaries with several broken teeth.

Locality and Horizon.—MR-6 locality, Verdigris Coulee, approximately 30 km east of the village of Milk River, southern Alberta; upper member of the Milk River Formation (Aquilan), Upper Cretaceous.

Known Distribution.—Upper Cretaceous Milk River Formation (Aquilan), southern Alberta.

Description.—UALVP 29787 (Fig. 31D) is a short, slender, and delicate dentary (7 mm long as preserved) that abruptly tapers anteriorly and ends at a weak mandibular symphysis. The lateral surface of the dentary is smooth and much less convex than that of *Colpodontosaurus cracens*. As in the latter species, the anteroventral edge of the dentary turns sharply medially, forming part of the floor of Meckelian canal. Four inferior alveolar foramina (mental foramina) are small and unequally spaced from one another.

Medially, the dentary bears a delicately built but prominent

subdental shelf, which is nearly equal in thickness along its extent; in *Colpodontosaurus cracens,* the shelf is much less prominent and thins posteriorly. The sulcus dentalis is absent in this specimen, as in *C. cracens.* The Meckelian canal narrows sharply anteriorly, and turns ventrally. The ventral border of the dentary bears an articular surface for the splenial, which indicates that the splenial extended anteriorly to about the midpoint of the tooth row, leaving a long and ventral opening of the Meckelian canal anteriorly. As in *Colpodontosaurus cracens,* the intramandibular septum lacks a free ventral border, but bears a small ventral process; however, this process is much less prominent than that of *Colpodontosaurus cracens.*

The preserved portion of the dentary bears broken bases and spaces for 13 teeth. The four tooth bases that are preserved show that the teeth are short and thin-walled, and have swollen and nonstriated bases. The dentary tooth row is incomplete, but can be estimated as having about 16 positions, significantly fewer than in *Colpodontosaurus cracens.* Every tooth has a small, circular basal foramen, which is medioposterior in position.

Another specimen (UALVP 33383; Fig. 31E), also a right dentary from the MR-6 locality, has one tooth and the broken bases for seven others preserved. This specimen is slightly larger and more robust than UALVP 29787, but it can be referred to the same species on the basis of thin-walled teeth and a horizontally wide but dorsoventrally slender subdental shelf.

Discussion.—The two specimens (UALVP 29787, 33383) are referrable to the Necrosauridae* on the basis of their general tooth morphology and dentary structure (e.g., thin-walled teeth and poorly developed intramandibular septum). Although the two dentaries are not well preserved, the significance of this discovery is obvious, as the specimens document the earliest North American fossil record of the Necrosauridae*, and represent an Aquilan species that was closely related to the Lancian *Colpodontosaurus cracens* (Fox [1972*a,* in schedula] recognized this relationship by identifying UALVP 29787 as "*Colpodontosaurus*? sp."). The Milk River specimens share with the Lancian *Colpodontosaurus cracens* character states such as having thin-walled, low-crowned, and nonstriated teeth, and a small ventral process on the weakly developed intramandibular septum; but differ from the latter (at the generic level) in having a significantly shorter dentary with a much more prominent subdental shelf. These morphological differences, combined with the 18 Myr chronologic gap between Milk River and Lance horizons, suggest that the Milk River form represents a new genus and species; however, the new taxon is not named in this paper, because the two specimens described above are too poorly preserved for an adequate diagnosis.

Genus *Parasaniwa* Gilmore, 1928

Type Species.—*Parasaniwa wyomingensis* Gilmore, 1928.

Range.—Upper Cretaceous, North America.

Diagnosis.—As for the type species.

Parasaniwa wyomingensis Gilmore, 1928 (Fig. 32A–H)

Parasaniwa obtusa Gilmore, 1928:26, fig. 10, 12.

Holotype.—USNM 10797, fragmentary left dentary having one complete and two broken teeth, collected by J. B. Hatcher in 1892 from the Lance Formation, eastern Wyoming (see Gilmore, 1928; Estes, 1964, 1983*a*).

Referred Specimens.—Frenchman Formation, Wounded Knee locality: UALVP 33347, premaxillary with two teeth; UALVP 33348, right maxillary fragment with two teeth; UALVP 33349, incomplete left dentary having ten tooth positions; UALVP 33350, dorsal vertebra. Scollard Formation, KUA-1 locality: UALVP 33384, fragmentary maxillary with two teeth.

Lance Formation, BTB locality: UALVP 33351–33353, incomplete tooth-bearing maxillaries; UALVP 33354, frontal; UALVP 1612, 1616, 33355, 33356, incomplete tooth-bearing dentaries. Hell Creek Formation, BCA locality: UALVP 33357–33360, tooth-bearing maxillary fragments; UALVP 33361, and several unnumbered dentaries; UALVP 33362, 33363, toothed pterygoids; UALVP 33364, 33365, parietals.

Known Distribution.—Upper Cretaceous Lance, Hell Creek, Frenchman, and Scollard formations (all Lancian). Congeneric specimens are also known from the Oldman Formation (Judithian), southern Alberta (see later description and discussion).

*Diagnosis (Revised from Estes, 1983*a*).*—Late Cretaceous necrosaurid lizard from North America, differing from *Necrosaurus* Filhol, 1876, and other necrosaurids in having skull osteoderms fused, flattened, and separated by shallow and wide grooves; maxillary having higher and vertically-directed dorsal process, which rises abruptly behind narial opening; marginal teeth strongly compressed laterally, trenchant, but lacking serrations; tooth bases dilated and having pronounced basal striations.

Description.—Gilmore (1928) gave an excellent description of the holotype dentary from the Lance Formation. Estes (1964) revised the description on more nearly complete specimens, and for the first time described and figured maxillary, frontal, and parietal materials of this species from the same formation. The following description focuses on the specimens in UALVP collections, especially on those from the Scollard and Frenchman formations, central Alberta and southwestern Saskatchewan, where the newly discovered specimens indicate a northern extension of the geographical distribution of this species. Other specimens from the BTB and BCA localities are included in this study as comparative materials from the same horizon but different geological formations.

Premaxillary. UALVP 33347 (Fig. 32A) from the Wounded Knee locality, Frenchman Formation, is the first premaxillary specimen to be described for *Parasaniwa wyomingensis.* The premaxillary is a single unit (unpaired), having five tooth posi-

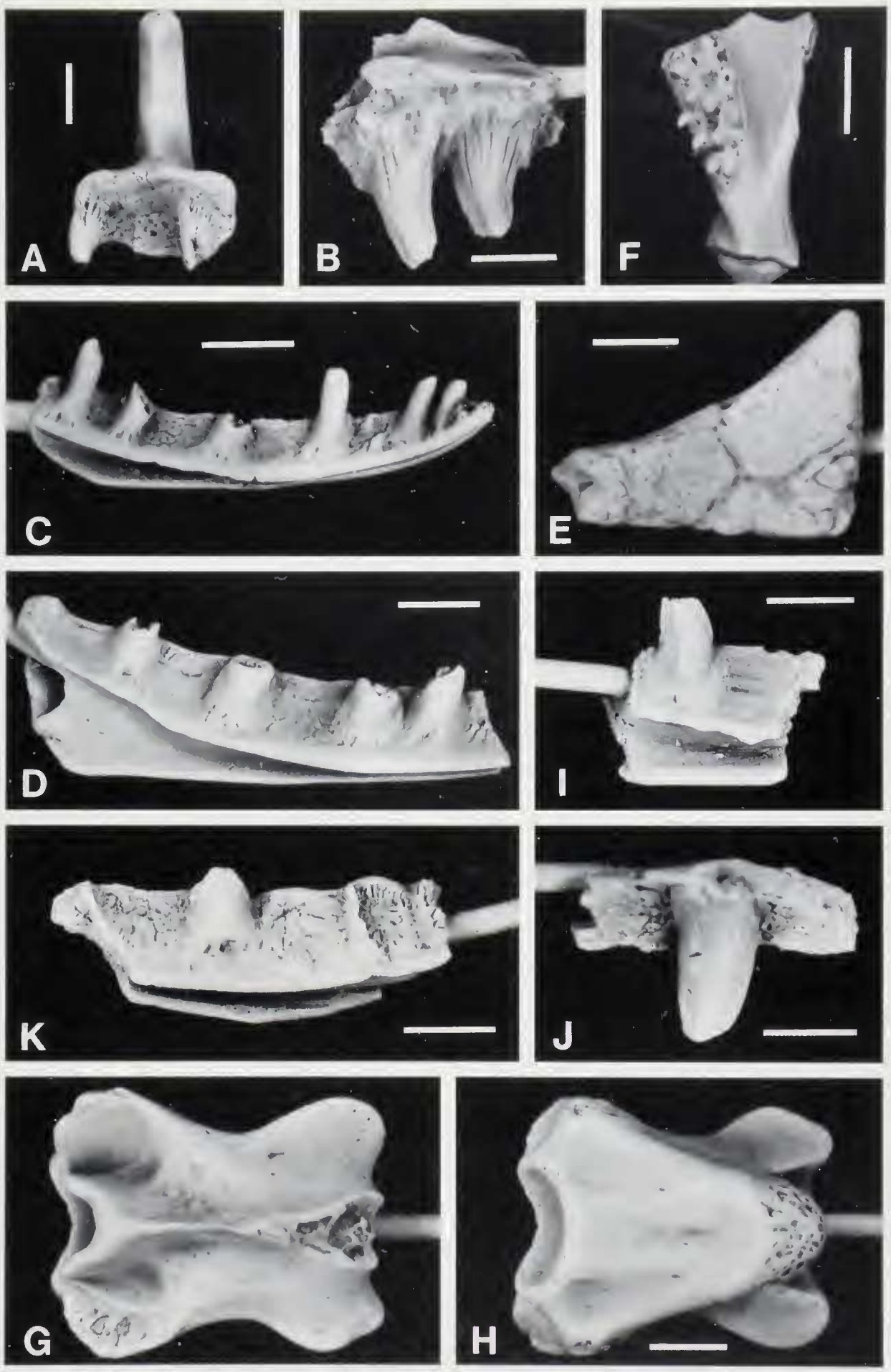

Fig. 32.—*Parasaniwa wyomingensis*, Lancian formations in Alberta, Saskatchewan, and Wyoming: A, UALVP 33347, incomplete premaxillary, lingual view; B, UALVP 33384, right maxillary fragment, medial view; C, UALVP 33349, left dentary, medial view; D, UALVP 33361, left dentary, medial view; E, UALVP 33354, right frontal, dorsal view; F, UALVP 33362, toothed left pterygoid, ventral view; G, H, UALVP 33350, dorsal vertebra, dorsal and ventral views. ?*Parasaniwa* sp., Milk River Formation, Alberta: I, UALVP 33923, fragmentary left dentary, medial view; J, UALVP 33924, left maxillary fragment, medial view; K, UALVP 33925, right dentary fragment, medial view. Scale = 2 mm.

tions. Two poorly preserved teeth show basal infoldings, the same tooth form as seen in the maxillary and dentary specimens. Dorsally, the premaxillary spine is tall, splint-like, and slightly recurved in correspondence with the high postnarial process of the maxillary. On each side of the base of this spine are two well-defined premaxillary foramina, through which passed nerves and blood vessels to the bases of the premaxillary teeth. Although no osteoderms are shown on the premaxillary, this specimen is different from the premaxillary of *Paraderma* in having a narrow and tall splint-like spine, and lacking a plate-like palatal process; and different from *Colpodontosaurus* and *Provaranosaurus* in the presence of basal striations on the teeth. Therefore, this specimen is here referred to *Parasaniwa.*

Maxillary. UALVP 33384 (Fig. 32B) consists of a fragmentary tooth-bearing right maxillary from the Scollard Formation, central Alberta. The two teeth preserved in front of the posterior interior alveolar foramen are short and strongly trenchant, but have no serrations on their anterior and posterior blades. The tooth bases are strongly expanded and striated with basal infoldings (Estes, 1964, noted that the degree of these striations is individually variable within the species). The supradental shelf is flat and horizontal, lacking a thickened dorsal fold, and the lateral wall of the maxillary is thin and shows no fused osteoderms, in these aspects differing from the maxillary of *Paraderma* (see later description). Other maxillaries from the Frenchman, Lance, and Hell Creek formations numbered above are referred to *Parasaniwa wyomingensis* on the basis of their tooth form and/or sculpture pattern on the lateral surface of the maxillaries.

Dentary. Among the dentary specimens referred to this species, two (UALVP 33349, 33361) are more extensively preserved than others. UALVP 33349 (Fig. 32C) is a left dentary from the Wounded Knee locality, Frenchman Formation. The specimen as preserved has ten tooth positions, including four teeth and the bases as well as spaces for six others. These teeth are pleurodont (contra Estes, 1964: "subpleurodont"), as only half or less of the tooth height projects above the lateral parapet of the jaw. The dentary shows the same configuration and structure as does UCMP 46041, a nearly complete dentary from the Lance Formation (see Estes, 1964:fig. 61): it is slender, lightly built, has a delicate symphyseal process, and a crescentic tooth-bearing border (see Estes, 1964:129). However, the Frenchman dentary is much smaller and more slender than UCMP 46041, indicating that it is from a young individual.

The other dentary (UALVP 33361; Fig. 32D), also from the left side, is from the BCA locality, Hell Creek Formation. This specimen reinforces Estes' statement that "the intramandibular septum is fused to the floor of the Meckelian groove throughout its length, and has a small notch posteriorly for Meckel's cartilage" (Estes, 1964:129); and, together with other specimens (UCMP 46041, UALVP 1612), shows that the groove for the anteromedial process of the coronoid bone is developed below the last four tooth positions, where the tooth-bearing border suddenly becomes narrow.

Frontal. UALVP 33354 (Fig. 32E) and another unnumbered specimen in the UALVP collections are clearly referrable to this species, as they show the same osteodermal pattern as the parietals of *P. wyomingensis* (see Estes, 1964). UALVP 33354 is a right frontal broken away from the left side at the midline. The unnumbered frontal from the same locality is similarly preserved. Estes (1964) described a fused frontal (AMNH 8103) with the midline suture clearly visible ventrally. Discovery of the new specimens from the BTB locality (Lance Formation) indicates that fusion of the frontals is an ontogenetic character for this species.

Parietal. Two specimens (UALVP 33364, 33365) from the BCA locality are identified as parietals of *Parasaniwa wyomingensis*: they are closely similar to UCMP 54200 (Estes, 1964: fig. 63), a well-preserved parietal from the type Lance Formation. Although the two parietals are poorly preserved both in terms of completeness and sculpture pattern, their general shape, size, and especially the lateral flange for the temporal musculature indicate that they belong to the same species as UCMP 54200.

Pterygoid. Two small pterygoid fragments, UALVP 33362, 33363 from the BCA locality, are referrable to *Parasaniwa wyomingensis.* Both of the specimens are too slender to be referrable to *Paraderma* or *Palaeosaniwa,* but are consistent with the maxillaries and dentaries referred to *Parasaniwa wyomingensis* from the same locality. Both specimens show that the pterygoid of this lizard is toothed, a primitive character state. UALVP 33362 (Fig. 32F) clearly shows that the pterygoid of *Parasaniwa* differs from that of helodermatids (e.g., UALVP 33338; see later description) not only in size and robustness, but more importantly, in the manner that the pterygoid teeth are arranged: the pterygoid teeth of *Parasaniwa* are arranged along the medial border of the palatine process, while those of helodermatids are inset from the border.

Vertebra. UALVP 33350 (Fig. 32G, H) and several unnumbered vertebrae from the Wounded Knee locality are referrable to *Parasaniwa wyomingensis.* UALVP 33350 is a well-preserved dorsal vertebra, which is clearly different from that of *Palaeosaniwa* in having a much weaker diapophysis below the prezygapophysis, and in having a much less constricted condylar base. In addition, UALVP 33350 and several unnumbered specimens are obviously too small to be referrable to *Palaeosaniwa* or *Paraderma*; they are consistent in size with the jaw materials for *Parasaniwa.*

Discussion.—Based on fragmentary dentary material from the Lance Formation, Gilmore (1928) founded *Parasaniwa,* and designated *P. wyomingensis* as the type species. His *Parasaniwa* included another species, *P. obtusa,* from the same locality. He separated the latter species from the type species on the basis that "it differs from the single complete tooth known of *P. wyomingensis* from the same formation and locality in having an erect crown (not recurved) with an obtusely pointed apex, and with striations restricted to the extreme basal surfaces" (Gilmore, 1928:86). Estes (1964) correctly placed *P. obtusa* in synonymy with *P. wyomingensis,* and recognized that the obtuse crown of *P. obtusa* is the result of erosion, and the degree of basal striations is variable for this lizard. A comparison of a large number of specimens in the UALVP collections shows that larger individuals have stronger basal striations than the smaller ones, indicating that this variation is an ontogenetic character. Here, we add another point in support of Estes' revision: the maxillary that Gilmore placed in *Parasaniwa obtusa* (USNM 10800; see Gilmore, 1928:pl. XXVI, fig. 10) shows obviously stronger basal striations than

his holotype dentary (USNM 10798), and is indistinguishable in structure from those later referred to *P. wyomingensis* (see Estes, 1964, and this paper).

The familial assignment of *Parasaniwa* has been changed since Gilmore's (1928) original description. Gilmore (1928) first placed *Parasaniwa* in the family Varanidae, but noted its striking similarity in tooth form to *Palaeovaranus* Filhol, 1877, which is a junior synonym of *Necrosaurus* Filhol, 1876 (see Hoffstetter, 1943; Estes, 1983*a*). Later, McDowell and Bogert (1954:32) accepted Gilmore's familial designation of *Parasaniwa* as a saniwine varanid, but noted that "there is a suggestive similarity in dental form between *Exostinus lancensis* and its contemporaries and compatriots *Parasaniwa obtusa* and *P. wyomingensis.*" In fact, a trenchant crown pattern is a character state shared by many carnivorous anguimorphans. Estes (1964) erected a new family, Parasaniwidae, which includes both *Parasaniwa* and *Paraderma,* and diagnosed the family as including genera that are "characterized by teeth with simple basal fluting extending into the medullary cavity; development of an intramandibular jaw hinge; unretracted nares; skull roof with well-defined scute areas; scutes tending toward multiplication" (Estes, 1964:128). Later, Hoffstetter (1969) recognized the close relationships between Parasaniwidae and Necrosauridae* on the evidence from maxillary structure and skull osteoderms, and suggested that the differences between the two groups are not great enough to separate them at a familial level. Accepting Hoffstetter's interpretation and on more extensive discussion with other colleagues, Estes (1983*a*) synonymized his Parasaniwidae with Necrosauridae* Hoffstetter, 1943, and tentatively allocated *Paraderma* to the Helodermatidae Gray, 1837 (see later discussion on *Paraderma*). The new specimens from several localities at Lancian horizons add no new information concerning the familial affiliation of this lizard; thus, in this paper *Parasaniwa wyomingensis* remains a Cretaceous necrosaurid as Estes (1983*a*) classified it.

The geologic distribution of *Parasaniwa wyomingensis,* in current understanding, is limited to Lancian horizons. The specimens of this particular species were previously known from the Lance and Hell Creek formations (Gilmore, 1928; Estes, 1964; Estes et al., 1969), and now from the Frenchman and Scollard formations (Fox, 1989; and this paper). Post-Lancian *Parasaniwa* sp. has been reported by Hecht (1959) from Eocene deposits in Wyoming, and by McKenna (1960) from the Eocene of Colorado. However, these materials likely belong to another genus (Estes, 1983*a*); accordingly, the Eocene record of *Parasaniwa* is rejected. Pre-Lancian congeneric materials have been reported in faunal lists from the Oldman Formation of Alberta (Fox, 1976; Currie, 1986; Eberth, 1987; Koster et al., 1987), but these Judithian materials likely represent another species (see below).

Three fragmentary specimens (UALVP 33923–33925) from the Milk River Formation are *Parasaniwa*-like, as they have laterally compressed teeth with a trenchant cutting blade and weak basal infoldings. However, these specimens are poorly preserved, and cannot be definitely referred to *Parasaniwa*; they are identified as "?*Parasaniwa* sp." (see Fig. 32I–K).

Parasaniwa, **new species**, cf. *P. wyomingensis* (Fig. 33)

Specimens.—UALVP 33346, 33366–33369; RTMP 65.24.6, 81.38.4; and 27 unnumbered specimens, all incomplete maxillaries. UALVP 33370–33373, RTMP 79.8.631, and more than 30 unnumbered fragment specimens, all dentaries; UALVP 33374, frontal; UALVP 33375–33377, RTMP 82.20.36, 84.168.2, parietals.

Locality and Horizon.—The specimens listed above are collected from various localities of the Oldman Formation, southeastern Alberta; the UALVP specimens are from the Irvine locality; and the RTMP specimens are from the Railway Grade, White Rock Coulee, Hope Johnson's microfossil site (DPP), Sandy Point, and Manyberries localities (coordinates on file in UALVP and RTMP).

Description.—All of the specimens listed above can be distinguished from those referred to *Palaeosaniwa* or *Paraderma* (see later description), and can be recognized as *Parasaniwa*-like on the basis of general jaw proportions, tooth form, or texture of osteodermal sculptures. Several relatively well-preserved specimens are described as follows.

Maxillary. UALVP 33346 (Fig. 33A, B) is a nearly complete right maxillary from the Irvine locality, Oldman Formation. In proportions and sculpture pattern generally this specimen is *Parasaniwa*-like, but differs from that of the type species (*P. wyomingensis*) in having a roughly triangular dorsal process and a greater number of tooth positions anterior to the posterior interior alveolar foramen (seven vs. five for *P. wyomingensis* in UCMP 49935, personal observation). Anteriorly, the two premaxillary processes are short and not clearly separated from each other, because the notch between them is poorly developed. The anterior interior alveolar foramen is small, rounded, and opens entirely on the internal side of the nasal process, so that it is clearly visible in medial view. The nasal process (= the dorsal or facial process of other authors) rises behind the narial opening at about a 45-degree angle, then curves along a gentle slope associated with the inward bending of the dorsalmost part of the process. There is no such step in UCMP 49935, but a vertical anterior

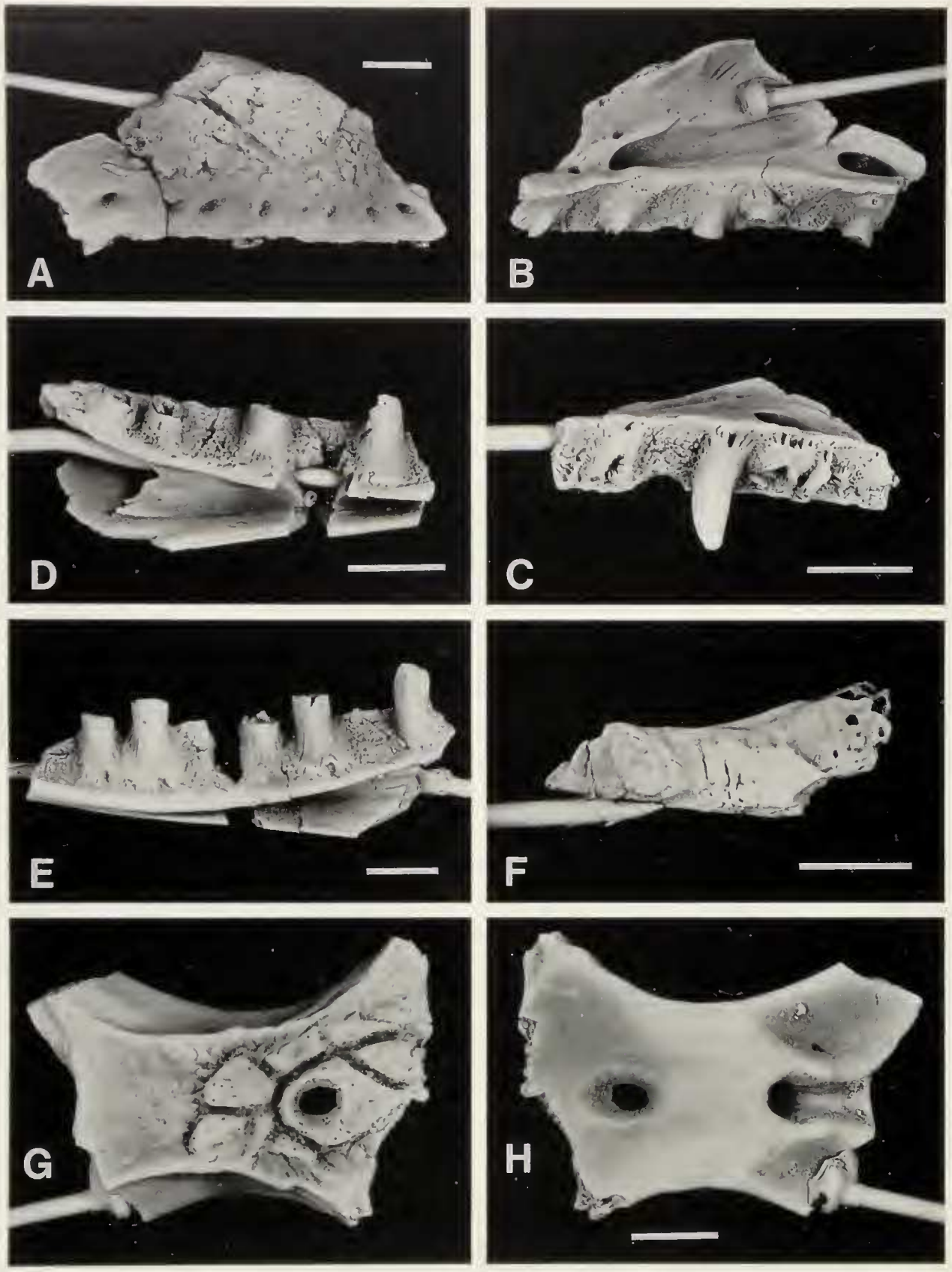

Fig. 33.—*Parasaniwa,* new species, cf. *P. wyomingensis,* Oldman Formation, Alberta: A, B, UALVP 33346, nearly complete right maxillary, lateral and medial views; C, RTMP 81.38.4, right maxillary fragment, medial view; D, UALVP 33370, posterior part of left dentary, medial view; E, UALVP 33371, right dentary, medial view; F, UALVP 33374, right frontal, dorsal view; G, H, UALVP 33375, incomplete parietal, dorsal and ventral views. Scale = 3 mm.

border of the nasal process (see Estes, 1964:fig. 62). The posterior border of the nasal process descends at a similar angle, giving the entire process a roughly triangular shape. UALVP 33346 is so far the most nearly complete maxillary known for *Parasaniwa* and is the best preserved with respect to the texture of the osteodermal sculpture. The lateral surface of the nasal process is vertically oriented, except for the medial curvature dorsally. The surface above the superior alveolar foramina is extensively covered with vermiculate osteoderms that are fused to the bone beneath (see Fig. 33A). The superior alveolar foramina, as many as eight, are small and open anteroventrally.

Internally, the maxillary bears a well-developed supradental shelf, which is a flat, shelf-like structure lacking the fold seen in *Paraderma.* As in *Parasaniwa wyomingensis* (UCMP 49935), a long trough-like depression for the nasal cavity above the shelf extends posteriorly and terminates in front of the posterior interior alveolar foramen (see Fig. 33B). However, the foramen opens above the eighth tooth position, while that in *P. wyomin-*

gensis opens above the sixth position (personal observation). The eight tooth positions preserved include the bases of five and the spaces for three others. The tooth bases have simple and short basal infoldings, as in the Lancian *Parasaniwa wyomingensis*. The posterior end of the maxillary is broken, so that the total number of maxillary teeth is unknown, but it can be estimated as 11–, since four or five positions are often seen along the tooth row posterior to the posterior interior alveolar foramen.

RTMP 81.38.4 (Fig. 33C) is a fragmentary right maxillary from White Rock Coulee (Sec. 16, Tp. 17, R 3, W 4), about 50 km north of Medicine Hat. The fragment shows one complete tooth, which is trenchant and slightly recurved, as in *Parasaniwa wyomingensis* (UALVP 33368 from the Irvine locality shows the same type of tooth form). This maxillary fragment also shows that there are at least four positions for teeth behind the posterior interior alveolar foramen.

Dentary. Among the dentaries referred to this species, two specimens from the Irvine locality (UALVP 33370, 33371) are better preserved than the others. UALVP 33370 (Fig. 33D) consists of the posterior half of a left dentary, which is broken directly in front of the sixth tooth position from the rear. This specimen shows that the intramandibular septum of this Judithian species remains fused to the floor of the Meckelian canal through most of its length, with only the posteriormost end having a weak separation. This is the same condition as seen in Lancian specimens, indicating that there has been little change in this aspect of dentary structure for the approximately 11 Myr known for the evolution of *Parasaniwa*. However, the tooth-bearing border of the Judithian species is much less crescentic than that in the Lancian *P. wyomingensis*. The tooth bases in UALVP 33370 have simple basal infoldings, as in the Lancian specimens. The lateral surface of the dentary is smooth and more nearly flat than convex. The last inferior alveolar foramen opens lateral to the third posteriormost tooth position.

Another specimen, UALVP 33371 (Fig. 33E), is an even better preserved right dentary, but the intramandibular septum is broken. The tooth bases have the same kind of infoldings as UALVP 33370, but these are stronger, as this is a larger specimen from a presumably older individual. On five of the teeth the crowns are broken, but one (second to last of the complete tooth row) is nearly complete. This tooth has strongly trenchant, blade-like cutting edges, but no serrations can be seen. These dentary teeth are pleurodont, having the lower half of the tooth height attached to the high lateral parapet of the dentary.

Frontal. UALVP 33374 (Fig. 33F) from the Irvine locality is an incomplete right frontal referred to *Parasaniwa* on the basis of its thin, large patches of osteoderms. Once again, this specimen shows that the frontals of *Parasaniwa* are paired, and the fused condition (Estes, 1964) is likely an ontogenetic character. On the ventral side of the frontal, the subolfactory process (flange) is well developed, but seems not to meet at the ventral midline.

Parietal. Five parietals from the Oldman Formation are referrable to this Judithian species on the basis of the general shape of the parietal table and the texture of the osteoderms; these include UALVP 33375 (Fig. 33G, H), 33376, 33377 from the Irvine, RTMP 82.20.36 from the Railway Grade, and RTMP 84.168.2 from the Sandy Point localities. All four specimens have the parietal table well preserved, but the temporal process is broken. These specimens together indicate that the parietal of this Judithian species is similar to that of Lancian *Parasaniwa wyomingensis* in general proportions and osteodermal pattern, but differs from the latter in having both the parietal foramen and the parietal fossa in a more posterior location and the fused osteoderms covering only the anterior two-thirds or less of the parietal table.

Discussion.—The specimens described above represent a Judithian lizard that is referrable to *Parasaniwa*, as they show close resemblances to the type species, *Parasaniwa wyomingensis*, in general jaw proportions, tooth morphology, and osteodermal pattern. However, this Judithian form differs from the type species in having a roughly triangular dorsal process of maxillary, less crescentic tooth-bearing border of dentary, a more posterior location for the parietal foramen, and a less extensive covering of fused osteoderms on the parietal. The parietal foramen in the Judithian specimens is close to the center of the parietal table, while that on the Lancian specimens (e.g., UCMP 54200; see Estes, 1964:fig. 63) is close to the frontoparietal suture; the fused osteoderms on the Judithian specimens cover only the anterior two-thirds or less of the parietal table, while those on the Lancian specimens are more extensive, covering two-thirds. These differences are so consistent on all the four specimens in the collection that they cannot be regarded as individual variations (or sexual dimorphism). Instead, the morphological differences plus the 11 Myr-chronologic gap from *P. wyomingensis* suggest that the Judithian specimens represent another species. However, we are unable to name this new species at present, because none of the known dentaries is complete enough to be compared to that of Lancian *P. wyomingensis*; similarly, the new species is represented by well-preserved maxillary material, while in Lancian *P. wyomingensis*, the maxillary is poorly known. Discovery of a better preserved dentary may reveal more significant characters for this new species.

Family Helodermatidae Gray, 1837

The Helodermatidae have the only two living species of venomous lizards: *Heloderma horridum* Wiegmann, 1829 (the Mexican beaded lizard) and *Heloderma suspectum* Cope, 1869 (the Gila monster), which have a restricted present-day distribution in southwestern United States and Mexico. The monophyly of the family is well supported by some 23 synapomorphies (Estes et al., 1988), among which the well-recognized osteologic characters are: teeth with venom grooves (Odermatt, 1940); and osteoderms thick, subconical, polygonal, and covering the entire body (McDowell and Bogert, 1954).

Contrary to their poor diversity and restricted distribution today, the fossil record of Helodermatidae

or helodermatid-like forms in North America, Europe, and Asia "suggest[s] that they inhabited a once broader spectrum of environments than would be inferred from their present distribution" (Pregill et al., 1986:199). Among the fossil forms, *Paraderma* Estes, 1964, has been recognized as the earliest definite record for the family (Pregill et al., 1986); later records include *Eurheloderma* Hoffstetter, 1957, from the upper Eocene of France, and indeterminate helodermatids are known from the lower Eocene of Belgium and the lower Oligocene of France (Rage and Augé, 1993); and *Lowesaurus* Pregill et al., 1986 and *Heloderma taxana* Stevens, 1977, from the Oligocene and Miocene of Colorado, Nebraska, and Texas. In addition, *Gobiderma* Borsuk-Bialynicka, 1984, and *Estesia* Norell et al., 1992, are known from the Gobi; they are in some degree related to the Helodermatidae, but their classification is still an open question (Borsuk-Bialynicka, 1984; Norell et al., 1992).

Genus *Paraderma* Estes, 1964

Type Species.—*Paraderma bogerti* Estes, 1964.
Range.—Upper Cretaceous, North America.
Diagnosis.—As for the type species.

Paraderma bogerti Estes, 1964 (Fig. 34, 35)

Holotype.—UCMP 54261, incomplete left maxillary with four broken teeth and the spaces for two others.

Type Locality and Horizon.—UCMP loc. V-5817 (False Disciple Point), Niobrara County, Wyoming (Clemens, 1963; Estes, 1964); Upper Cretaceous Lance Formation (Lancian).

Referred Specimens.—Scollard Formation, KUA-1 locality: UALVP 29845 and several unnumbered specimens, tooth-bearing dentaries; UALVP 33385, incomplete parietal; UALVP 33902–33910, disarticulated cervical and dorsal vertebrae. Frenchman Formation, Wounded Knee locality: UALVP 29846, incomplete right dentary; and UALVP 33387, dorsal vertebra.

Known Distribution.—Upper Cretaceous Lance Formation, eastern Wyoming; Hell Creek Formation, eastern Montana; Scollard Formation, central Alberta; and Frenchman Formation, southwestern Saskatchewan (all Lancian). Pre-Lancian distribution of the species is reported from the Judith River Formation (Sahni, 1972), but see later discussion.

Diagnosis (Revised from Estes, 1983a).—A Late Cretaceous helodermatid from North America, differing from other fossil and extant forms of the same family by a combination of the following character states: marginal teeth robust, trenchant crown having shallow anterior but no posterior venom groove; parietal foramen present, but small; cephalic osteoderms polygonal, with pitted sculpture and separated by wide groove; neural spines on trunk vertebrae tall and vertically directed.

Description.—Several specimens in the UALVP collection from the KUA-1 locality provide significant material for a better understanding of *Paraderma bogerti*. The specimens described below include a parietal, several vertebrae, and limb bones that are the first known for this species, and a well-preserved dentary bearing teeth with an anterior venom groove.

Dentary. Among the dentaries referred to *Paraderma bogerti* in this paper, two are well preserved. The first, UALVP 29845 (Fig. 34A; 35A, B), is a left dentary from the KUA-1 locality, Scollard Formation. The specimen is anteriorly complete, having the symphyseal part well preserved, but is broken posteriorly at the tenth tooth position. Nevertheless, it is the best dentary specimen known for this species. Anteromedially, the dentary bears a prominent symphyseal process, corresponding with the strong medial curvature of the jaw and making the mandibular arch widely U-shaped. The subdental shelf and the sulcus dentalis are entirely absent; instead, a robust tooth-bearing border forms most of the medial side of the Meckelian canal. The anterior half of the canal opens ventrally, but the posterior half gradually turns ventromedially in correspondence with the posterior deepening of the jaw. Because of breakage at the tenth tooth position, the nature of the intramandibular septum cannot be determined from this specimen (but see description of another specimen below).

UALVP 29845 shows the first nine tooth positions of the jaw, including the first, third, fifth, seventh, and eighth dentary teeth, and the spaces for the second, fourth, sixth, and ninth. This tooth-and-space pattern is obviously the result of an alternating pattern of tooth replacement. The first tooth on the jaw is mostly broken off, leaving only the basal part preserved. The eighth tooth is completely preserved, showing that the posterior teeth of this lizard are laterally compressed, having a trenchant crown without serrations. The remaining three teeth have the tips of the crowns broken off, but still show that the anterior teeth are more columnar than compressed. These teeth are pleurodont, having the lower half of the tooth attached to the lateral parapet of the jaw. In agreement with the holotype maxillary (UCMP 54261; see Pregill et al., 1986:fig. 9), the teeth in this dentary also show a taxonomically important character for this species: a clearly defined venom groove is developed anteriorly on the tooth shaft (see Fig. 34A), which is, however, less conspicuous and shallower than that in the extant *Heloderma*; and it has no posterior groove, differing from the latter genus. The tooth base is weakly infolded, and each tooth has a basal foramen developed medially.

The lateral surface of the dentary is smooth and is anteriorly strongly turned towards the mandibular symphysis in correspondence with the anterior curvature of the jaw. Four inferior alveolar foramina can be seen on the surface; and the fifth is not present, although the approximate location for this foramen is preserved on the jaw. These foramina are small in relation to the size of the jaw, and are slightly elongated and widely spaced from one another.

Another specimen, UALVP 29846 (Fig. 35C), is the posterior part of a right dentary from the Wounded Knee locality. Although fragmentary, this specimen has one tooth and the spaces for three others preserved; more importantly, the specimen clearly shows that the ventral border of the intramandibular septum

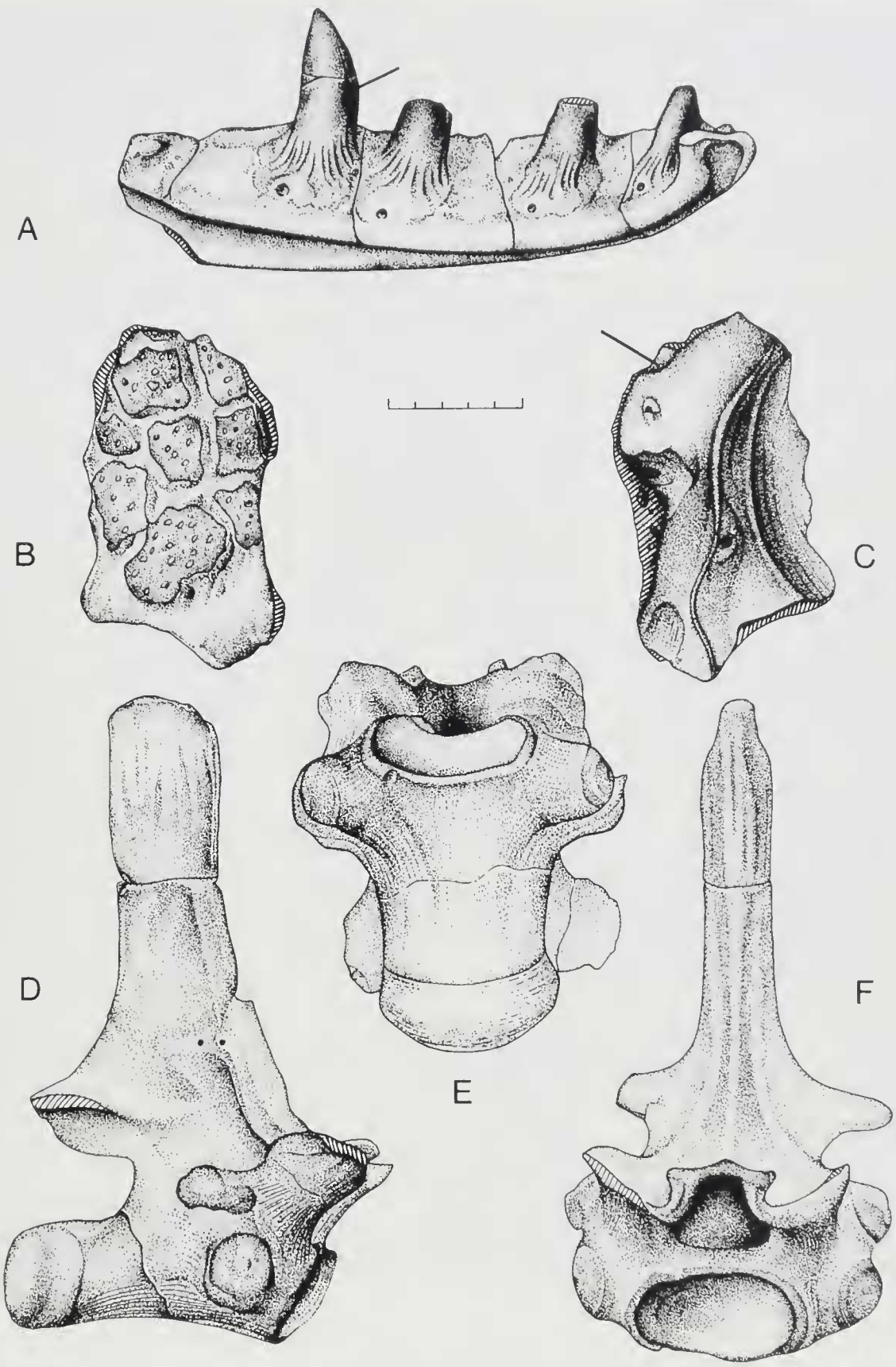

Fig. 34.—*Paraderma bogerti,* Scollard Formation, Alberta: A, UALVP 29845, nearly complete left dentary, medial view (arrow indicates venom groove); B, C, UALVP 33385, incomplete parietal, dorsal and ventral views (arrow indicates incomplete parietal foramen); D–F, UALVP 33903, dorsal vertebra, lateral, ventral, and anterior views. Scale = 5 mm.

is largely free from the floor of the Meckelian canal (contra Estes, 1983*a*:177), in contrast to *Parasaniwa* from the same horizon in which the septum is mostly fused to the floor of the canal.

Parietal. UALVP 33385 (Fig. 35D, E) is the first parietal known for *Paraderma bogerti,* since previous referral of YPM 1063 to this species (Estes, 1964) was erroneous (see later discussion). Although incomplete with only the left side preserved, the specimen clearly shows a helodermatid synapomorphy: origin of the adductor muscles from the ventral surface of the parietal table (Pregill et al., 1986), as indicated by a strong roof-like lateral flange. The lateral border of the bone is comparatively straight (not strongly concave medially), indicating that the parietal must have been roughly trapezoidal in shape. The dorsal surface of the bone is covered with heavy osteoderms that in pattern and surface texture are similar to those on the holotype maxillary (Estes, 1964:fig. 64; Pregill et al., 1986:fig. 9). Another

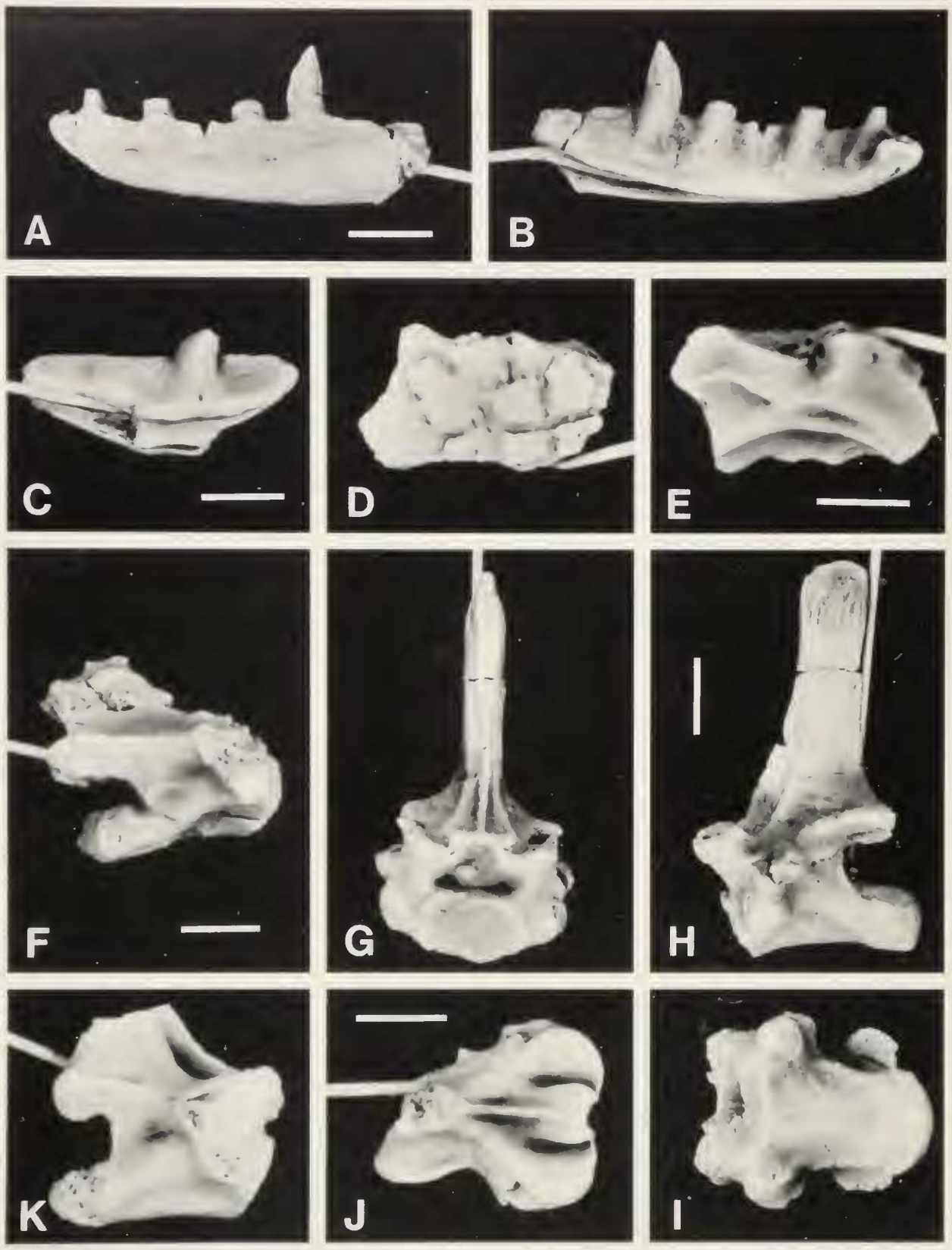

Fig. 35.—*Paraderma bogerti,* Scollard and Frenchman formations, Alberta and Saskatchewan: A, B, UALVP 29845, nearly complete left dentary, lateral and medial views; C, UALVP 29846, fragment of right dentary, medial view; D, E, UALVP 33385, incomplete parietal, dorsal and ventral views; F, UALVP 29902, cervical vertebra, lateral view; G–I, UALVP 29903, complete dorsal vertebra, anterior, lateral, and ventral views; J, K, UALVP 33387, dorsal vertebra, dorsal and lateral views. Scale = 5 mm.

taxonomically and evolutionarily significant feature that this parietal shows is the presence of a small but clearly defined parietal foramen (Fig. 34C), which is close to the frontoparietal suture in position. In all extant and Tertiary forms in which the parietal is known, the foramen is absent.

Vertebra. Nine disarticulated vertebrae from the KUA-1 locality and one from the Wounded Knee locality are referrable to *Paraderma bogerti* on the basis of their general helodermatid morphology (see below). One of these (UALVP 33902; Fig. 35F) can be identified as a cervical vertebra, as it has a relatively low and wide neural spine compared to other vertebrae. This cervical shows no hypapophysis on the ventral surface of the centrum, and absence of the hypapophysis is considered as a synapomorphy for the Helodermatidae (Hoffstetter and Gasc, 1967, 1969; Pregill et al., 1986; Estes et al., 1988). The remainder are well-preserved dorsal vertebrae, having a more or less tapered centrum, and a condyle with a poorly developed flange. They are definitely of helodermatid type, as they have a slightly concave lateral border of the centrum, and in the posterior half of the centrum, the lateral borders are subparallel (Hoffstatter and Gasc,

1969; Pregill et al., 1986). The neural spine is narrow and tall, but is vertically directed on the dorsal vertebrae, rather than rising at an acute angle as in other helodermatids (Pregill et al., 1986). In addition, the dorsal vertebrae of *Paraderma bogerti* differ from those of *Palaeosaniwa canadensis* and other varanids in having a less pronounced precondylar constriction, an anteriorly oriented condylar cup, and well-developed zygantra and zygosphenes. These character states are clearly shown on UALVP 33903 (Fig. 34D–F, 35G–I) from the KUA-1 locality, and UALVP 33387 (Fig. 35J, K) from the Wounded Knee locality. Another important feature that these vertebrae show is that the diapophysis and parapophysis are separated; the condition in extant *Heloderma* in this aspect has not been clearly described in previous publications to our knowledge, but Boulenger's (1891:fig. 5) figure seems to show that the two processes in *Heloderma* are jointed to form a synapophysis (sensu Romer, 1956), as in varanids.

Limb Bone. An unnumbered right humerus from the KUA-1 locality is so far the only limb bone known for *Paraderma*. Although not articulated, the humerus was preserved close to the vertebrae described above: its proximal end is about 10 mm away from a dorsal verteba in the claystone matrix. The following characters are used to distinguish the humerus of *Paraderma* from that of other large varanoids: the humerus is robustly built, with a short shaft and weakly expanded proximal and distal ends. The proximal articular surface is wide and suboval in outline, and the deltoid crest is short and nearly perpendicular to the long axis of the proximal articular surface, differing from the condition in *Saniwa* and *Varanus* (see Gilmore, 1922). The distal end of this humerus lacks well-ossified condyles and an ectepicondylar foramen, which are present in the two varanids mentioned above (see Gilmore, 1922).

Discussion.—Estes (1964) founded *Paraderma bogerti* on several specimens from the Lance Formation, Wyoming. The holotype (UCMP 54261; see Estes, 1964:fig. 64) is a nearly complete left maxillary with thick osteoderms fused to its lateral surface. As Estes (1964, 1983*a*) stressed, the obvious characters for this form are the *Heloderma*-like osteoderms on the maxillary and the strong medial curvature of the nasal process. However, in contrast to Estes' (1964:133) statement that "internally the maxillary is identical with that of *Parasaniwa,*" the holotype of *Paraderma bogerti* differs from the maxillary of *Parasaniwa* in having a great dorsal thickening of the supradental shelf, which forms a strong fold of the shelf, and having double openings for the superior alveolar canal (personal observation).

The dentary morphology of *Paraderma bogerti* is poorly known, as previous collections include only one dentary fragment (UCMP 49939), which was briefly described and figured (Estes, 1964; Pregill et al., 1986:fig. 8). The newly discovered specimens from the Scollard and Frenchman formations reveal, contrary to what Estes (1964, 1983*a*) presumed, that the teeth of this lizard are much more high-crowned (UALVP 29845) than those of *Parasaniwa,* and the intramandibular septum is free from the floor of the Meckelian canal (UALVP 29846). The dentary of *Paraderma* is clearly distinguishable from that of *Parasaniwa* from the same horizon: in addition to its much larger size and massiveness, the dentary of *Paraderma* has a more robust but less crescentic tooth-bearing border, much stronger symphyseal process, and a free ventral border of the intramandibular septum, while the septum in *Parasaniwa* is mostly fused to the floor of the Meckelian canal (Estes, 1964).

Estes (1964) originally placed *Paraderma* together with *Parasaniwa* in his Parasaniwidae (= Necrosauridae* Hoffstetter, 1943) "on the basis of general tooth form [which was largely unknown then] and simple basal infolding of tooth bases" (Estes, 1964:134); he also noted close resemblances to *Heloderma* in premaxillary morphology, snout shape, and osteodermal pattern. Accepting Hoffstetter's (1969) interpretation that Parasaniwidae and Necrosauridae* are closely related groups, and recognizing the incipient venom groove on the teeth of *Paraderma,* Estes (1983*a*) synonymized Parasaniwidae with Necrosauridae*, and allocated *Paraderma* to the Helodermatidae, albeit with some uncertainty. That *Paraderma* is a helodermatid has been confirmed by a more recent revision of fossil helodermatids (Pregill et al., 1986).

The discovery of the parietal of *Paraderma bogerti* (UALVP 33385) is of special importance, as it provides solid evidence to clarify some taxonomic and evolutionary controversies concerning the Helodermatidae. Gilmore (1928:158) placed an incomplete parietal (YPM 1063) from the Lance Formation that Marsh (1892:450) had referred to *Chamops segnis* as "the upper part of the cranium" in his "*Megasaurus robustus*" (this name is a nomen dubium, although Estes, 1983*a* listed it as the synonym of *Palaeosaniwa canadensis*). Estes (1964: 135; 1983*a*:95, 177) referred YPM 1063 to *Paraderma bogerti,* but ambiguously commented that it "appears to belong to *Palaeosaniwa* as shown by the UCMP specimen of the latter." With the discovery of UALVP 33385, the characters of which demonstrate a taxonomic association with the holotype maxillary of *Paraderma bogerti,* the referral of YPM 1063 to *P. bogerti* is probably in error. In fact, Gilmore's (1928:pl. 27, fig. 3) figure shows that YPM 1063 is certainly not helodermatid-like, since its strongly developed lateral flange indicates that the temporal musculature originated from the dorsolateral surface, while in helodermatids the

temporal muscles are attached to the ventrolateral surface of the parietal table (Pregill et al., 1986). Alternatively, an association of YPM 1063 with *Palaeosaniwa,* as Estes (1983*a*) suggested, is possible but quite uncertain, because skull elements of *Palaeosaniwa* are poorly known.

The vertebrae of *Paraderma bogerti* were previously unknown (Pregill et al., 1986). With the discovery of well-preserved vertebrae of this species from the Scollard and Frenchman formations, now it is possible to draw the following conclusions: The vertebrae of *Paraderma* share with those of other helodermatids character states such as a constricted neural canal and a laterally compressed centrum; however, they are distinguishable from those of other forms (e.g., *Lowesaurus*; see Pregill et al., 1986: fig. 5) in having much stronger zygantra and zygosphenes, and the narrow and tall neural spine, at least in the dorsal vertebrae, is vertically directed (contra Pregill et al., 1986: neural spines rising at an acute angle as a diagnostic feature for the Helodermatidae).

A Tertiary (upper Eocene or lower Oligocene) European helodermatid, *Eurheloderma* Hoffstetter, 1957, is characterized by having an elongate parietal that is strongly constricted in its middle portion (Hoffstetter, 1957; Estes, 1983*a*; Pregill et al., 1986). Yatkola (1976) regarded the constricted parietal as a derived condition, but lacked support from fossil evidence. Pregill et al. (1986:190) pointed out that Yatkola's consideration "may be correct, but the parietal of *Paraderma* must be found to verify the polarity." Now, with the discovery of UALVP 33385, it is clear that a wide and trapezoidal parietal is a primitive condition in the Helodermatidae. This statement is also supported by the discovery of another helodermatid parietal from the Oldman Formation (see later description on "Helodermatidae, genus and species undetermined").

Genus *Labrodioctes,* **new genus**

Etymology.—Labros + *dioktes* (Greek, masculine), meaning "greedy hunter," in reference to the presumed predatory habit (feeding style) of this helodermatid.

Type and Only Known Species.—Labrodioctes montanensis, new species.

Range.—Upper Cretaceous, North America.

Diagnosis.—As for the type and only known species.

Labrodioctes montanensis, **new species** (Fig. 36A–D)

Holotype.—ANSP 18664, incomplete left dentary having five teeth and spaces and broken bases of six others.

Type Locality and Horizon.—Blackbird Ridge site, in NW 1/4, Sec. 6, Tp. 7, R 20, Golden Valley County, central Montana; Upper Cretaceous Judith River Formation (Judithian).

Referred Specimen.—RTMP 78.18.1, a fragmentary frontal with thick, fused osteoderms; this referral is tentative, since the specimen is anatomically noncomparable to the holotype dentary and is from a different locality.

Known Distribution.—Upper Cretaceous Judith River Formation, eastern Montana; Oldman Formation, southeastern Alberta (both Judithian).

Diagnosis.—A large helodermatid differing from *Paraderma* as follows: teeth nontrenchant, strongly recurved, having posterior venom groove; dentary tooth-bearing border thickened, strongly curved ventrally. Differing from all other helodermatids by having the following character states: dentary greatly elongate but robustly built; marginal teeth lacking anterior venom groove; posterior groove shallow, only extending to half of crown height.

Description.—The holotype, ANSP 18664 (Fig. 36A), is a large, robust dentary of about three times the size of the dentary of *Paraderma.* The specimen is anteriorly complete, but has a broken surface lateral to the seventh through 11th tooth positions. The dentary has a robust, crescentic tooth-bearing border, which is more strongly dorsoventrally concave than in *Paraderma,* but the curvature is not as strong as in extant *Heloderma.* The anterior end of the bone strongly curves to the mandibular symphysis and bears a prominent medioposterior projection (the symphyseal process). The anterior half of the Meckelian canal is an extremely shallow sulcus that opens ventrally, curving to the strong mandibular symphysis. The posterior half of the canal is greatly deepened and triangular in medial view, widely open medially with the splenial missing. A well-developed intramandibular septum posteriorly separates the Meckelian canal from the lateral inferior alveolar canal. The septum is posteriorly broken, but the preserved part has a free ventral border, as in Lancian *Paraderma* (see above description). The posterior notch for the Meckelian cartilage is not preserved on this specimen.

As preserved, the dentary has 11 tooth positions, including five teeth (four complete and one with broken tip), three broken bases, and three vacant spaces as a result of tooth replacement. The dentary teeth are robust, having greatly thickened and fluted bases, and pointed and strongly recurved crowns. Although the tooth crowns have weak anterior and posterior cutting edges (without serrations), they are not laterally compressed and are nontrenchant compared to those in *Paraderma bogerti.* The fifth and the seventh have a shallow groove on the posteromedial surface of the teeth. These are probably venom grooves, which are different from the grooves of other helodermatids: other fossil and extant helodermatids have a clearly defined anterior venom groove extending to or near the tooth apex, whereas the groove on ANSP 18664 is shallow and postcromedial, and only extends to half of the crown height. These teeth are widely spaced from each other and are pleurodont, having the upper half of the tooth height projecting above the lateral parapet of the jaw. The last two tooth positions on the preserved part of the dentary are associated ventrally with a sudden narrowing of the tooth-bearing

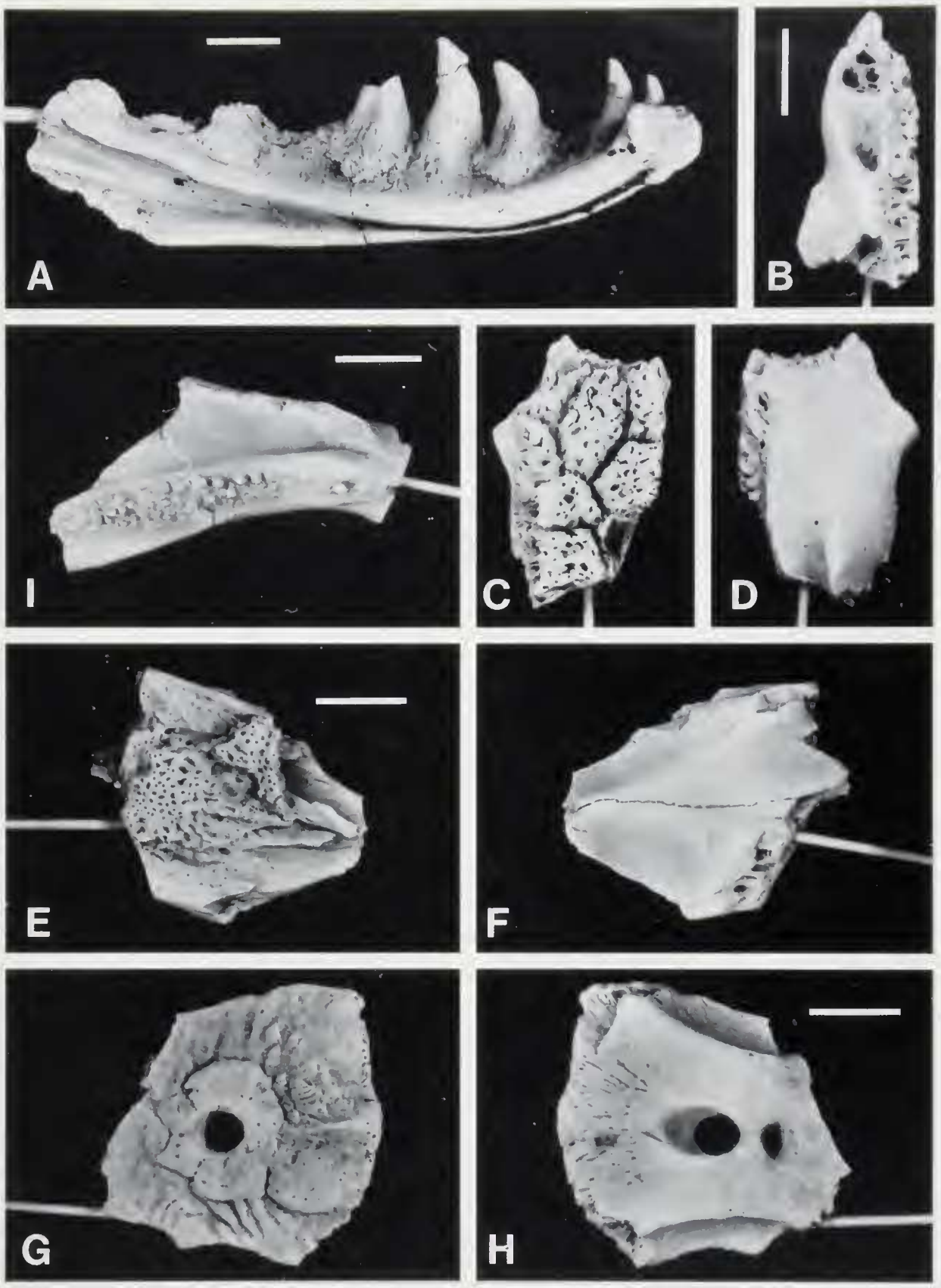

Fig. 36.—*Labrodioctes montanensis,* new genus and species, Judith River and Oldman formations, Montana and Alberta: A, ANSP 18664 (holotype), incomplete left dentary, medial view; B–D, RTMP 78.18.1, incomplete left frontal, lateral, dorsal, and ventral views. Helodermatidae, genus and species undetermined, Oldman Formation, Alberta: E, F, RTMP 88.36.212, incomplete frontals, dorsal and ventral views; G, H, RTMP 85.58.58, incomplete parietal, dorsal and ventral views; I, UALVP 33338, toothed left pterygoid, ventral view. Scale = 6 mm.

border, where the anterior inferior alveolar foramen is located. This condition, plus the free ventral border of the intramandibular septum, indicates that probably only the posteriormost one or two teeth are missing from this specimen, yielding a total count of about 12–13 for the dentary tooth row.

The lateral surface of the dentary is mostly preserved, with the posterodorsal part broken. The surface is smooth, more flat than convex, and anteriorly turns medially to the mandibular symphysis. The four lateral mental foramina (lateral inferior alveolar foramina) that open to the surface are about equal in size and are evenly spaced from one another. These foramina are more or less almond-shaped, and are horizontally aligned along the middle depth of the jaw.

RTMP 78.18.1 (Fig. 36B–D), a robust frontal from White

Rock Coulee, is compatible in size with ANSP 18664, and is definitely helodermatid-like in having thick, polygonal osteoderms fused to the skull elements (McDowell and Bogert, 1954), and the prefrontal and postfrontal incisions approaching each other above the orbits (Estes et al., 1988; see Fig. 36B). The Oldman Formation in Alberta is geologically equivalent to the upper part of the Judith River Formation in Montana (e.g., L. S. Russell, 1964; Eberth and Hamblin, 1993). Therefore, ANSP 18664 and RTMP 78.18.1 may pertain to the same species, unless another helodermatid of that size within the same geologic and geographic range is involved (for which there is no evidence).

Discussion.—The dentary described above (ANSP 18664) represents a Judithian varanoid, as it bears teeth with basal infolding, which is a varanoid synapomorphy (see Estes et al., 1988). Moreover, ANSP 18664 is *Paraderma*-like, as it shows a robust tooth-bearing border that is strongly curved dorsomedially at the anterior end. However, the specimen is very large and elongate, and is different from Lancian *Paraderma* in having a much stronger mandibular symphysis, and strongly recurved, much less trenchant teeth that lack an anterior venom groove. These differences are great enough to separate it from *Paraderma bogerti* at the generic level. The lack of an anterior venom groove on the dentary teeth may weaken its referral to the Helodermatidae, as the presence of such a groove is regarded as one of the few unambiguous synapomorphies for the family (Bogert and del Campo, 1956; Estes et al., 1988; but see also Norell et al., 1992); however, several other character states strongly support a placement of it within the family. These include: a robust and medially curved tooth-bearing border, strong mandibular symphysis with a prominent process, and robust teeth that are broadly based and weakly infolded. On the basis of these character states, *Labrodioctes montanensis* is tentatively placed in the family Helodermatidae, while the lack of an anterior venom groove should be regarded as a primitive condition in the family (and it now is clear that the Lancian *Paraderma* has a weaker groove than Tertiary and Recent helodermatid species).

Mesozoic helodermatid or helodermatid-like fossils are uncommon. Besides the Lancian *Paraderma bogerti* and Judithian *Labrodioctes montanensis* from North America, *Gobiderma pulchra* Borsuk-Bialynicka, 1984, and *Estesia mongoliensis* Norell et al., 1992, are known from the Barun Goyot Formation (late Campanian in age, Fox, 1978; Jerzykiewicz and Russell, 1991), East Asian Gobi Desert. The holotype of *Gobiderma pulchra* (ZPAL MgR-III/64) is a nearly complete skull with a partial mandible from the Khermeen Tsav II locality. Although she noted the helodermatid similarities of this Gobi species in general morphology of the skull, osteodermal pattern, and construction of the jaw, Borsuk-Bialynicka (1984:39) placed *Gobiderma* in "necrosaurian grade, family uncertain." In a review of helodermatid evolution, Pregill et al. (1986) emphasized that *Gobiderma* is more generalized in skull morphology than *Heloderma,* and stated that "the overall appearance of the skull recalls that of *Xenosaurus*" (Pregill et al., 1986:195). From personal examination of the holotype and referred specimens of *Gobiderma pulchra,* we here offer the following comments: 1) *Gobiderma* is definitely a varanoid, but not a xenosaurid, because it has plicidentine infoldings of the tooth bases (Borsuk-Bialynicka, 1984; personal observation). 2) *Gobiderma* shares several characters that are in combination unique to helodermatids: the jaw adductors have a ventral origin on the parietal; the supradental shelf curves medially anteriorly; the osteoderms are tuberculate and fused to the skull elements; and the tooth number is reduced in correspondence with the shortening of the jaws. 3) However, *Gobiderma* differs from all known helodermatids in having a more pointed and longer snout, and in retaining a supratemporal opening.

From the above comparisons, *Gobiderma* appears to be more closely related to the Helodermatidae than to any other varanoids. We agree with Borsuk-Bialynicka (1984), who regarded *Gobiderma* as "an Asian substitute of the American helodermatids," and not ancestral to the extant American helodermatids. North American Mesozoic helodermatids are mostly based on disarticulated jaws and skull elements while the teeth of *Gobiderma* are poorly known; therefore, the precise relationships and taxonomic status of *Gobiderma* will remain obscure until further study of better preserved materials for both North American and Asian forms.

No matter whether or not the East Asian *Gobiderma* and *Estesia* are included in the Helodermatidae, the North American Judithian *Labrodioctes* represents the earliest fossil record for the family, because the age of the Barun Goyot Formation in the Gobi Desert is probably younger than the Judith River and Oldman formations (e.g., Fox, 1978; Jerzykiewicz and Russell, 1991).

Genus and species undetermined
(Fig. 36E–I)

Specimens.—RTMP 88.36.212, incomplete partially fused frontals; RTMP 85.58.58, incomplete parietal; UALVP 33338, a left pterygoid.

Locality and Horizon.—See description of each specimen below.

Description.—The incomplete partially fused frontals, RTMP 88.36.212 (Fig. 36E, F), from the Railway Grade locality, are roughly triangular in outline as preserved, and are covered with patches of pitted osteoderms. In structure and thickness, these osteoderms are different from those on RTMP 78.18.1 (described above), but are compatible with those on a parietal described below. Although anteriorly broken, symmetrical articular surfaces on both sides indicate that the nasal extended posteriorly to overlap the frontals. Pre- and postfrontal incisions are not preserved, and it cannot be determined whether or not the pre- and postfrontals were in contact above the orbit. The frontals are posteriorly broken, and thus the nature of the frontoparietal suture is unknown. In ventral view, the specimen shows a midline suture and breakage at the anterior end of the left subolfactory process such that the morphology of the process is unknown.

RTMP 85.58.58 (Fig. 36G, H), also from the Railway Grade locality, consists of the main body of a parietal table, with the posterior part and the supratemporal processes broken off. The parietal is broad and trapezoidal, lacking a strong constriction of the middle part of the table. Besides its large size and different texture of osteoderms, this parietal differs from that of *Parasaniwa* in having the parietal fossa (ventral view) close to the parietal foramen, and more importantly, in having a roof-like dorsolateral extension for the attachment of temporal musculature to the ventral surface of the parietal table (see Fig. 36H). The latter feature is one of the characters that distinguish helodermatids from varanids (Pregill et al., 1986). In ventral view, the specimen shows a small but deep parietal fossa, which is proportionally much smaller than that in *Paraderma bogerti* and is more closely located to the parietal foramen. The specimen is distinguishable from the parietal of *Paraderma* by its large size, large parietal foramen at the center of the parietal table, and thin, rounded tuberculate osteoderms. The parietal of *Paraderma* has a smaller parietal foramen close to the frontoparietal suture, and thick, polygonal osteoderms divided by deep grooves. Although collected from roughly the same horizon, this parietal is not compatible in size and robustness with the dentary and referred frontal of *Labrodioctes* (see above); therefore, it probably represents a helodermatid other than *Labrodioctes.*

UALVP 33338 (Fig. 36I) was collected by D. Brinkman from the bank of the South Saskatchewan River, about 8 km upstream from Sandy Point. The specimen is the anterior part of a toothed left pterygoid that can be tentatively referred as to "Helodermatidae, genus and species undetermined" based on its significantly large size and *Heloderma*-like morphology. On this specimen, the basal plate is well preserved, and the anteromedial (or palatine) process is nearly complete, with only the anterior tip broken. The process is short and broad, having an anteromedial depression for the pterygoid–palatine articulation. The anterolateral (or ectopterygoid) process is broken off from the basal plate; however, the specimen clearly shows a triangular ventral depression between the diverging palatine and ectopterygoid processes; such a triangular depression indicates a short and wide skull, as it is developed in *Heloderma,* but not in *Lanthanotus* and *Varanus,* in which the skull tends to be longer and more slender. The posterior (or quadrate) process, arising in front of the pterygoid–basisphenoid contact, is also missing. Posteriorly from the anterior part of the palatine process, the pterygoid bears a heavily toothed area parallel but inset from the medial border of the basal plate. The teeth are fused to the plate in an apparently random manner such that no particular pattern can be recognized.

Discussion.—The general morphology of RTMP 85.58.58 clearly indicates that the parietal is helodermatid-like, as it shows a roof-like lateral flange for a ventral origin of the temporal musculature, and osteoderms are fused to the dorsal surface of the bone. However, the specimen is incompatible with RTMP 78.18.1 (frontal referred to *Labrodioctes*) in robustness and surface texture of the osteoderms, but in these aspects is compatible with the frontals (RTMP 88.36.212) from the same locality (compare Fig. 36C, E, G). Therefore, the parietal and the frontals probably represent another helodermatid of Judithian age. The parietal of *Labrodioctes montanensis* is unknown, but is likely to have been much more robust and to have had thicker and more dense osteoderms than in this specimen. In spite of its relatively large size, RTMP 85.58.58 is more lightly built than the parietal of *Paraderma bogerti,* which is only half the size of the former; and this Judithian form has a proportionally larger parietal foramen at the center of the parietal table, which represents a more primitive condition than in Lancian *Paraderma.*

As described above, the pterygoid UALVP 33338 is large and likely belongs to a helodermatid. The size and robustness of this specimen are compatible with both *Palaeosaniwa* and *Labrodioctes* (in both genera, the pterygoid is unknown), and the possibility of its association with the former genus cannot be ruled out at present. Here we tentatively refer this specimen to "Helodermatidae, genus and species undetermined" based on its helodermatid-like morphology, leaving its referral indefinitive pending study of more and better preserved materials when these become available.

Family Varanidae Gray, 1827

The extant varanids include approximately 34 species in the single genus *Varanus* Merrem, 1820, and are confined to the Old World, with a distribution in Australasia, southeast Asia, and Africa. Although absent from the New World today, fossil varanids have long been known from North America since Leidy reported *Saniwa ensidens* from the Eocene of Wyoming in 1870. In western Canada, *Palaeosaniwa canadensis* Gilmore, 1928, from the Oldman Formation in Alberta marks the earliest definite appearance of the Varanidae in North America, and may provide the earliest record of the family, pending on the age and relationships of *Telmasau-*

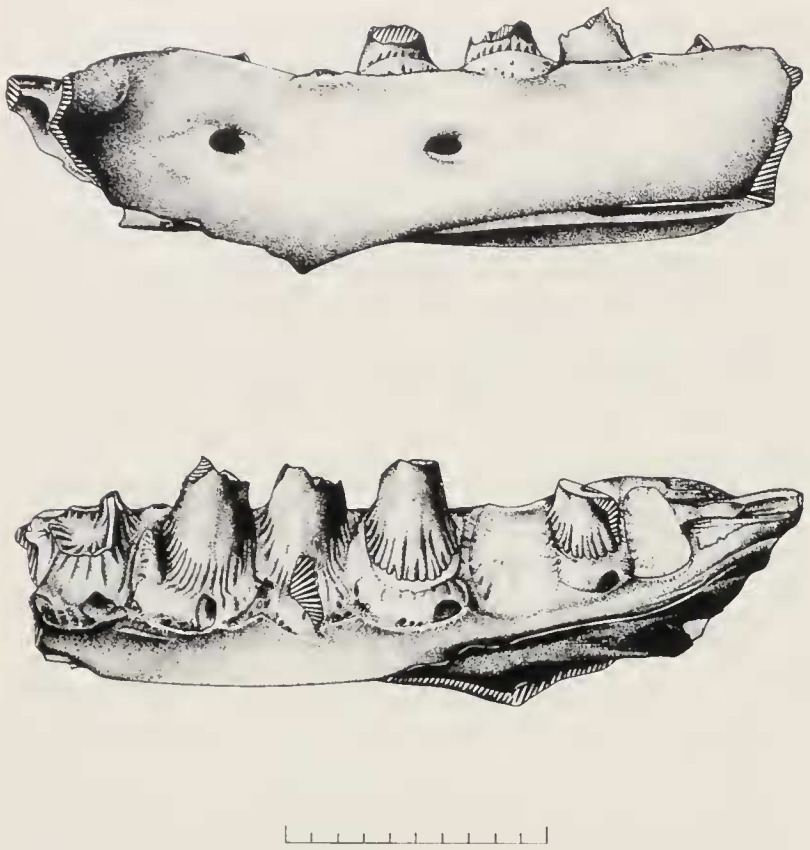

Fig. 37.—*Palaeosaniwa canadensis*, Oldman Formation, Alberta: RTMP 89.121.1, incomplete right dentary, lateral (above) and medial (below) views. Scale = 10 mm.

rus Gilmore, 1943, from the Djadochta Formation, Gobi Desert (see also Borsuk-Bialynicka, 1984).

Genus *Palaeosaniwa* Gilmore, 1928

Type Species.—*Palaeosaniwa canadensis* Gilmore, 1928.

Range.—Upper Cretaceous, North America.

Diagnosis.—As for the type and only known species.

Palaeosaniwa canadensis Gilmore, 1928 (Fig. 37, 38)

Megasaurus robustus Gilmore, 1928:pl. 27, fig. 1, 1a.

Holotype.—USNM 10864, a nearly complete dorsal vertebra collected by W. E. Cutler in 1913 from the Oldman (then Belly River) Formation "near Steveville" (Gilmore, 1928:84), southeastern Alberta.

Referred Specimens.—RTMP 80.29.120, 80.20.37, incomplete maxillaries; UALVP 33337, RTMP 85.36.184, 89.36.101, 89.121.1, tooth-bearing dentaries; RTMP 73.23.1, 80.16.439, 81.22.55, 81.26.22, 82.14.42, 82.19.106, 82.31.30, 85.43.24, 85.65.13, 85.67.24 (total: ten), and UALVP 33339–33345 (total: seven), all isolated vertebrae; RTMP 73.7.1, 81.23.47, tibiae.

Locality and Horizon.—The specimens listed above were collected from various localities of the Oldman Formation in southeastern Alberta; UALVP specimens are mostly from Sandy Point and nearby localities, and RTMP specimens are mostly from the Bonebed microfossil sites in DPP and nearby localities (coordinates on file in UALVP and RTMP).

Known Distribution.—Upper Cretaceous Oldman Formation, southeastern Alberta; Judith River Formation, Montana (Sahni, 1972; see discussion below). Post-Judithian occurrences of this species have been reported from the Lance Formation (Estes, 1964), Hell Creek Formation (Estes et al., 1969), and Fort Union Formation (Sullivan, 1982), but see discussion below.

Diagnosis (Revised from Gilmore, 1928; Estes, 1983a).—A Late Cretaceous large varanid from North America, closely resembling *Saniwa* Leidy, 1870, in vertebral morphology, but differing from the latter and Recent *Varanus* in having the following combination of character states: narial retraction short, restricted to three or four anteriormost tooth positions; marginal teeth relatively short, robust, and strongly recurved; tooth bases greatly expanded, crowns narrower, slightly trenchant, having microserrations on both anterior and posterior cutting edges; vertebral neural spines short and robust, rodlike, with strong anterior crest.

Description.—Among the specimens available for this study, several maxillaries and dentaries as well as other skull elements can be confidently referred to *Palaeosaniwa canadensis* on the basis of their large size (compatible with the size of the holotype vertebra) and varanid tooth form. These specimens are important for providing, for the first time, information about characters other than vertebrae, on which the species was primarily based and from which the species has been long known, except for isolated teeth reported by Estes (1964) from the Lance Formation.

Maxillary. Included in the collections for this study are two maxillaries that are the first known for *Palaeosaniwa canadensis*: RTMP 80.29.120 (Fig. 38A, B), a left maxillary fragment from Sandy Point, South Saskatchewan River, about 20 km south of Empress; and RTMP 80.20.37 (Fig. 38C, D), a right maxillary fragment from BB 118 microfossil site (DPP), southeastern Alberta.

The specimen RTMP 80.29.120 is especially important for it is the only known maxillary that bears a complete tooth of this species. The maxillary tooth is short, robust, and strongly recurved. The tooth base is greatly expanded and infolded, forming the so-called "honeycomb structure" (term used by Estes, 1964). A small, round foramen is developed at the medial side of the tooth base. From the expanded tooth base, the tooth is greatly reduced in its thickness towards the apex, but has a medially swollen shaft. The tooth crown is more or less laterally compressed, strongly recurved, and has slightly trenchant anterior and posterior edges that bear microserrations. The maxillary shows a well-developed posterior interior alveolar foramen, above and slightly posterior to the tooth that remains. This foramen indicates that the single tooth on the specimen is one of the posterior maxillary teeth, which may be slightly shorter and more robust than the teeth adjacent anteriorly, which are in the middle part of the tooth row. Although fragmentary, RTMP 80.29.120 shows that the lateral surface of the maxillary is or-

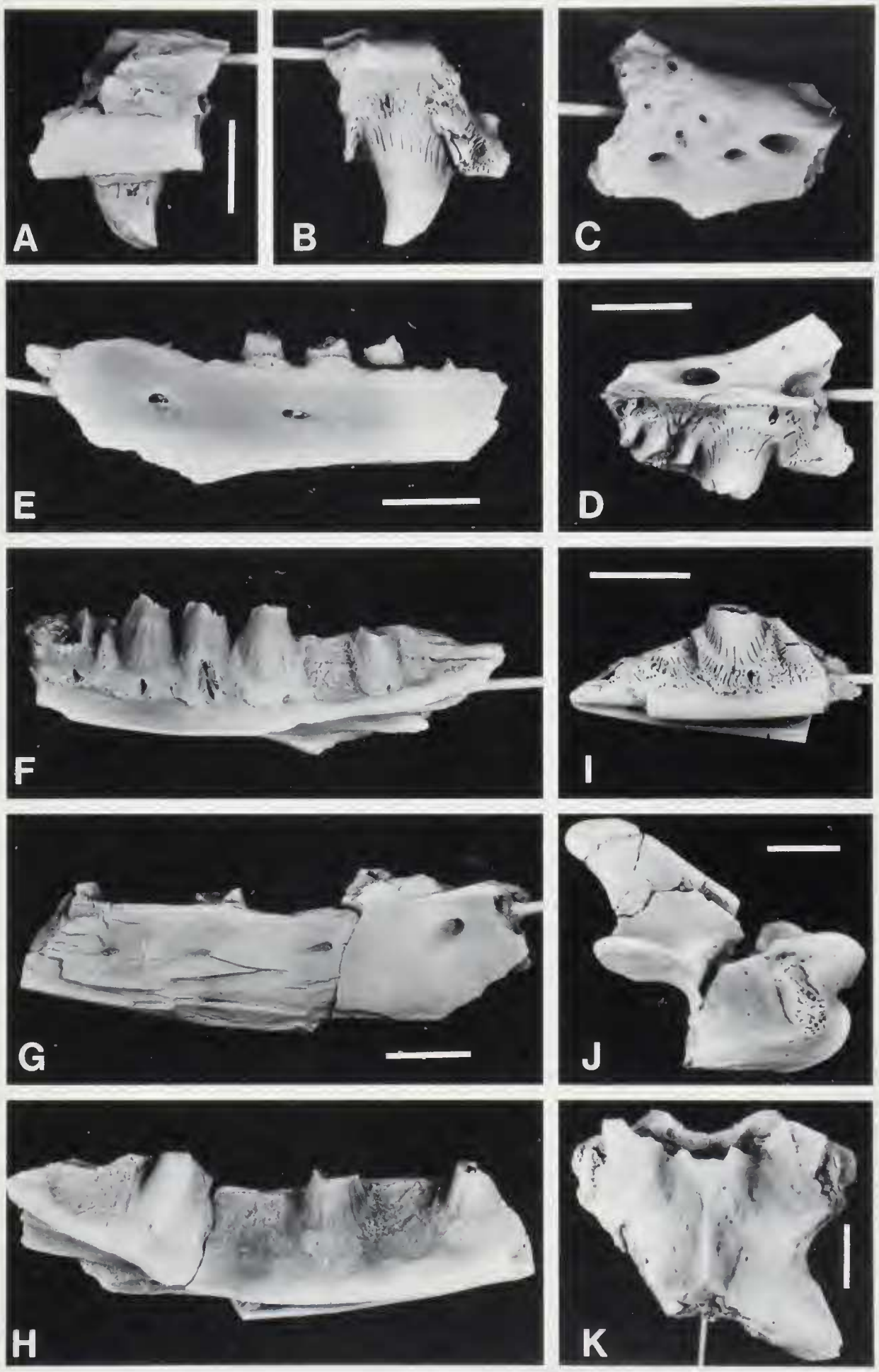

Fig. 38.—*Palaeosaniwa canadensis*, Oldman Formation, Alberta: A, B, RTMP 80.29.120, left maxillary fragment, lateral and medial views; C, D, RTMP 80.20.37, right maxillary fragment, lateral and medial views; E, F, RTMP 89.121.1, incomplete right dentary, lateral and medial views; G, H, RTMP 89.36.101, incomplete left dentary, lateral and medial views; I, RTMP 85.36.184, right dentary fragment, medial view; J, UALVP 33342, dorsal vertebra, lateral view; K, UALVP 33344, dorsal vertebra, dorsal view. Scale = 6 mm.

namented at least partially with bony rugosities that are in texture and thickness different from the fused osteoderms on the frontal and parietal of helodermatids from the same horizon (see foregoing description). Most varanids have osteoderms reduced or absent, and when present, they are not fused to the skull elements; however, *Varanus komodoensis* has heavy osteoderms bonded to skull elements (McDowell and Bogert, 1954:pl. 12).

RTMP 80.20.37 (Fig. 38C, D) is the anterior fragment of a right maxillary, which bears a broken tooth and the base of another. The maxillary has a strong base for the premaxillary process, and the facial process rises as a gentle slope behind this base. The length of the premaxillary process and the gentle slope of the nasal process are sharply different from *Parasaniwa,* but indicate a narial retraction to the point of the third or the fourth tooth position. Medial and anterior to the facial process is the anterior interior alveolar foramen, which is almost as large as the posterior interior alveolar foramen (shown on RTMP 80.29.120). This maxillary fragment also shows surface sculpture similar to that on RTMP 80.29.120 described above.

Dentary. In this study, four dentary specimens (RTMP 89.36.101, 89.121.1, 85.36.184, and UALVP 33337) are referred to *Palaeosaniwa canadensis.* The large size and robustness of these dentaries are consistent with the size and proportions of the holotype vertebra. The dentary teeth, having microserrations, are easily distinguishable from those of other North American Cretaceous varanoid taxa, such as *Paraderma* and *Parasaniwa.*

Among the four dentaries mentioned above, RTMP 89.121.1 (Fig. 37; 38E, F) from a locality (RTMP L1700) near Onefour, Alberta, is the best preserved in terms of showing tooth form and the dentary structure of this early varanid. This specimen has four broken teeth and the spaces for four others, representing the last eight positions of the dentary tooth row. Medially, as commonly seen in other varanoids, RTMP 89.121.1 shows that the dental gutter on the medial side of the tooth row is entirely lost, and the subdental shelf is replaced by a ventrally growing ridge that forms a crescentic tooth-bearing border; however, this border is much less crescentic than that of *Parasaniwa* and is different from that in helodermatids in having a sharp ventral edge. The Meckelian canal on this specimen is mostly open ventrally, with only the posterior portion below the last three teeth facing more medially than ventrally. A short but well-defined intramandibular septum is developed below the last three and one-half tooth positions. It has a free ventral border that is clearly separated from the floor of the Meckelian canal and is developed as a prominent ridge-like structure, differing in those respects from the septum in *Parasaniwa.* The posterior edge of the septum is deeply notched for the Meckelian cartilage. Dorsal to the intramandibular septum is the coronoid facet, a deep groove running under the posterior tooth-bearing border for an interlocking articulation with the internal anterior process of the coronoid bone. The facet extends anteriorly beyond the anterior end of the intramandibular septum by half of a tooth position; that is, the facet is located below the last four tooth positions.

Four teeth are preserved on RTMP 89.121.1, but all have the crown apex missing by breakage. The teeth are pleurodont, with half of their height attached to the lateral parapet of the jaw. As seen on the maxillary (RTMP 80.29.120), the tooth bases are greatly expanded and infolded with complex plicidentine. Each tooth has a basal foramen opening medially at a strong basal cement ring. The tooth shaft above the basal infoldings has a flattened lateral surface, but is medially swollen and anteriorly depressed, giving a roughly semicircular but anteriorly concave cross section (see Fig. 37). Although the tooth apices are all broken on this specimen, the parts that remain indicate that the crowns are laterally compressed and slightly recurved. Two teeth on the jaw (the six and seventh from the back) clearly show microserrations on the anterior cutting edge of the crown. The last three teeth are obviously smaller than those anterior to them. Anteriorly, the tooth-bearing border of this specimen curves dorsally, indicating that the anterior breakage is close to the mandibular symphysis. Judging from tooth size and the curvature of the tooth-bearing border, we estimate that the complete dentary tooth row of this lizard contained 11–12 positions.

The lateral surface of RTMP 89.121.1 is smooth with no osteodermal rugosities, and bears inferior alveolar foramina that are widely spaced from each other; the last foramen is located close to the last dentary tooth, as in extant *Varanus.* The lateral surface of this specimen is shallowly concave posterodorsally. The concavity in *Heloderma* houses the venom gland, while in other varanoids it houses a large seromucous gland (Bogert and del Campo, 1956; Kochva, 1974; Saint-Girons, 1976). The depression of *Palaeosaniwa* is probably for a seromucous gland, as there are no venom grooves developed on the dentary teeth of this lizard. In spite of this depression, the dentary is generally straight in dorsal view, lacking the distinct sigmoid curvature of helodermatids (McDowell and Bogert, 1954).

Of the other three dentaries referred to the same species, RTMP 89.36.101 (Fig. 38G, H) is an incomplete left dentary having six tooth positions (three broken teeth and the spaces for three others). The specimen shows that the jaw structure and the tooth form agree in every aspect with those of RTMP 89.121.1, except for its slightly larger size (perhaps indicating an older individual). The other two specimens (UALVP 33337 and RTMP 85.36.184) are both fragmentary right dentaries with broken teeth. UALVP 33337, from a site about 8 km upstream from Sandy Point, represents the largest individual among the four specimens. RTMP 85.36.184 (Fig. 38I) from BB 25 (DPP) clearly shows the basal infoldings and the cement around the tooth base. Both specimens show that the inner surface of the Meckelian canal is more deeply grooved than in the jaw of *Paraderma.*

Vertebra. As listed above, some 17 disarticulated vertebrae are referred to *Palaeosaniwa canadensis* on the basis of their resemblances in size and morphology to the holotype (USNM 10864) and other vertebrae that Gilmore (1928) described. There are no cervical vertebrae, as none of these show a hypapophysis, a structure that is diagnostic for the cervicals. Most of these are dorsal vertebrae, showing a morphology that is basically the same as Gilmore (1928) described; however, UALVP 33342 (Fig. 38J) has the neural spine completely preserved, which has previously been unknown in this species. The discovery of this vertebra supports Estes' (1964) interpretation that the spine is not expanded or plate-like, and in this aspect differs from *Saniwa* and extant *Varanus.* The zygantrum and zygosphene of these dorsal vertebrae are far less well developed than those in *Paraderma,* and are sharply distinguishable from the latter in having an arched neural canal in anterior view (best shown on UALVP 33344; Fig. 38K), while in *Paraderma,* the canal is compressed owing to the development of strong articular surfaces of the zygantrum.

RTMP 82.31.30 from BB 23 (DPP) is probably the only caudal vertebra in the available collections for this study. It differs from presacral vertebrae in having much weaker zygapophyses and basically no zygosphene. Ventrally, the centrum differs from that of the dorsal vertebrae in lacking a flattened surface but having a longitudinal groove between a pair of prominent ridges. The transverse processes are mostly broken off, but the preserved

bases indicate that they are posterolaterally directed and probably slender and short. The posterior half of the centrum is broken, and thus, neither the condyle nor the articulation for the chevron is preserved.

Tibia. Two specimens (RTMP 73.7.1, 81.23.47) from DPP are both left tibiae, and are referred to *Palaeosaniwa canadensis* on their compatibility in size with the vertebrae described above and resemblance to the tibia known for *Saniwa* (Gilmore, 1928). The two tibiae differ from that of *Varanus* in having a well-developed sigmoid crest laterally on the proximal end; *Saniwa* has a similar but longer and stronger crest at the same location (Gilmore, 1928:pl. 6). The distal end of RTMP 73.7.1 has a strong lateral condyle that extends well beyond the medial condyle and in this aspect differs from *Varanus*.

Discussion.—Gilmore (1928) founded *Palaeosaniwa canadensis* on four isolated dorsal vertebrae (UA 112; USNM 10864, 11045; GSC 8510). The type specimen (USNM 10864) that he selected for the species was collected by W. E. Cutler in 1913 from a site near Steveville, Red Deer River, southeastern Alberta. Gilmore's naming of *Palaeosaniwa canadensis* is significant, as it documents the first North American Mesozoic varanid recognized and the first discovery of a terrestrial lizard from the Oldman Formation. On the other hand, his naming of this lizard has created a long-term problem, because the species is founded solely on vertebral specimens, and vertebrae of lizards are much less diagnostic than jaw materials especially at lower taxon (generic and specific) levels. Accordingly, this lizard has long been poorly understood.

Gilmore (1928:83) placed *Palaeosaniwa canadensis* in the family Varanidae on the basis of "the tapering form of the centrum with constricted condylar end" and the general similarity compared to the vertebrae of *Saniwa* Leidy, 1870, a North American Eocene varanid. This familial assignment was questioned by McDowell and Bogert (1954:53), who stated that *Palaeosaniwa* "although definitely platynotan, [is] not positively varanid." However, Estes (1964) added tooth form (trenchant crown with microserrations plus complex basal infoldings) as new evidence to support the varanid affinity of *Palaeosaniwa*. Estes (1983*a*) cited a *Palaeosaniwa* skull associated with vertebrae in the UCMP collections; unfortunately, this important discovery has never been described or otherwise mentioned since.

In the present study, maxillary and dentary materials are described for the first time for this early varanid. These materials are obviously compatible in size with the vertebrae on which the species is founded, and are morphologically clearly distinguishable from homologous parts of *Parasaniwa, Paraderma,* and *Labrodioctes,* the three other known North American varanoids of the same age. Therefore, these specimens are referred to *Palaeosaniwa.*

Estes (1964) referred several vertebrae and isolated teeth from the Lance Formation to *Palaeosaniwa canadensis.* If the referral is correct, it will extend the geologic range of this varanid species from Judithian to Lancian. However, there are some uncertainties regarding the identification of the specimens: first, the isolated teeth without referrence to jaw structure are hard to demonstrate as different from those of *Saniwa* or other varanoids; and the "microserrations" that Estes (1964) figured seem too small and dense, compared to those on Oldman specimens described in this paper, to pertain to the same species. Second, the Lancian dorsal vertebrae (Estes, 1964:fig. 66) show much weaker diapophyses and a more convex ventral surface of the centrum than those from the Oldman Formation. These, plus a well-developed zygantrum and zygosphene, suggest that the Lancian vertebrae may represent a varanoid other than *Palaeosaniwa canadensis*; comparison should be made with helodermatids.

Estes et al. (1969) reported "*Palaeosaniwa,* cf. *P. canadensis*" from the Hell Creek Formation, eastern Montana. The specimen for this identification was a single large vertebra (MCZ 3665) that was neither figured nor described in detail. The specimen was characterized as having "convex lateral borders of the centrum, as do Eocene *Saniwa* and both Oldman Formation and Lance Formation *Palaeosaniwa*" (Estes et al., 1969:22); however, lack of information on the morphologies of the condylar cup, precondylar constriction, and neural spine prevents a definite referral of this specimen to *Palaeosaniwa.*

Sullivan (1982:1007) recorded "cf. *Palaeosaniwa canadensis*" from a fragmentary dentary (AMNH 15957) from the Fort Union Formation, Wyoming, and stated that "the labyrinthine morphology of the tooth bases is the major criterion for referring this specimen to *Palaeosaniwa canadensis.* Assuming the assignment is correct, *Palaeosaniwa*'s range is extended from the Late Cretaceous (Gilmore, 1928; Estes, 1964) to the middle Paleocene (Torrejonian)." It is clear now that presence of basal dentine infolding is broadly synapomorphic for Varanoidea (Estes et al., 1988), not a unique feature for *Palaeosaniwa canadensis*; and thus, both Sullivan's identification and his claim of a Paleocene record of cf. *Palaeosaniwa* are unconvincing. Estes (1983*a*:184) made the following comments on this matter: "The fragmentary nature of the speci-

men, as well as the fact that Sullivan gave no measurements or figure, makes any definite statement impossible." In fact, Sullivan (1982) reported a *Saniwa* vertebra from the same locality. From his description, however, we see no reason for assigning the vertebra to "cf. *Saniwa* sp." or the dentary fragment to "cf. *Palaeosaniwa canadensis.*" A more likely possibility is that the two specimens pertain to the same species (which would be "cf. *Saniwa* sp.").

GEOLOGICAL DISTRIBUTION AND EVOLUTION OF LATE CRETACEOUS LIZARDS IN WESTERN CANADA

Late Cretaceous lizards from western Canada were previously documented in scattered publications (see Introduction), but no synthetic studies have ever been attempted, largely owing to lack of fossil specimens. However, over the past 25 years collections from Alberta and Saskatchewan have provided important materials for undertaking the research reported in this paper. The purpose of this section is to summarize the fossil record of lizards from the Upper Cretaceous of western Canada, and to discuss the evolutionary changes through time of the relevant groups in the study area. The geological distribution of these lizards is summarized in the form of two charts (Fig. 39, 40), in which the radiometric ages are from Harland et al. (1990) and Thomas et al. (1990). In the following discussion, we recognize three lizard assemblages on the basis of differences in geological age and taxonomic composition.

Aquilan (Early Campanian) Assemblage

Aquilan, or early Campanian, lizards are known in western Canada from the upper member of the Milk River Formation, southern Alberta. The Milk River assemblage documents the earliest North American records for the families Iguanidae*, Scincidae, Xenosauridae, Necrosauridae*, and the earliest certain record of the Anguidae; and it also includes several early teiids (*Chamops, Sphenosiagon,* and, possibly, *Glyptogenys*).

Iguania.—The Milk River iguanians include *Cnephasaurus* and an unnamed new genus and species, which can be referred to the Iguanidae* (sensu lato, = nonacrodontan iguanians). In tooth mor-

Myr	Stage	NALM Age	Iguanidae	Teiidae	Scincidae	?Xantusiidae	?Cordylidae	Family incertae sedis
65	Maestrichtian	Lancian	Genus & species new (B)	*Chamops* *Leptochamops* *Meniscognathus* *Haptosphenus* *Stypodontosaurus*		Genus & species new (unnamed) *Contogenys*	Genus & species undetermined (B)	Genus & species new (A) Genus & species new (B)
	?–	Edmontonian		?*Chamops* sp.				
76	Campanian	Judithian		*Chamops* sp. *Socognathus* *Sphenosiagon* *Glyptogenys* *Gerontoseps* *Leptochamops*	*Orthrioscincus*		Genus & species undetermined (A)	Genus & species undetermined
83		Aquilan	*Cnephasaurus* Genus & species new (A)	*Chamops* sp. *Sphenosiagon* *Glyptogenys*	*Penemabuya* *Aocnodromeus*			Genus & species undetermined

Fig. 39.—Geological distribution of Late Cretaceous lizards in western Canada I—Iguania and Scincomorpha.

Myr	Stage	NALM Age	Xenosauridae	Anguidae	Necrosauridae	Helodermatidae	Varanidae
65	Maestrichtian	Lancian	*Exostinus*	*Odaxosaurus*	*Colpodontosaurus* *Parasaniwa*	*Paraderma*	
	— ? —	Edmontonian					
76	Campanian	— ? — Judithian	? *Exostinus* sp.	*Odaxosaurus*	*Parasaniwa* n. sp. cf. *P. wyomingensis*	Genus & species undetermined *Labrodioctes*	*Palaeosaniwa*
		Aquilan	Genus & species undetermined	Genus & species undetermined	Genus & species new (unnamed) ?*Parasaniwa* sp.		
83							

Fig. 40.—Geological distribution of Late Cretaceous lizards in western Canada II—Anguimorpha.

phology, *Cnephasaurus* closely resembles the extant *Crotaphytus,* a predatory crotaphytine found in southwestern United States, Mexico, and Central America. This resemblance indicates that, at least functionally, the dentition of *Cnephasaurus* is indicative of its grasshopper-hunting habit, whereas the phylogenetic significance of this resemblance cannot be verified at present. "The crotaphytines are remarkably plesiomorphic in many respects and lack any descriptive unique morphological features" (Frost and Etheridge, 1989:23). The unnamed new genus and species is recognized on a more fragmentary specimen, and its relationship with other iguanids is unknown.

Scincomorpha.—The Aquilan Teiidae are not as diverse as the Judithian and Lancian teiids, with only three taxa (*Chamops* sp., *Sphenosiagon,* and possibly *Glyptogenys*) recognized from relatively extensive sampling by screen washing. If not a result of taphonomic processes (Wilson, 1988: taphonomic loss), the relative paucity of teiids in the Aquilan assemblage may indicate that the major diversification of the group did not take place until mid-Campanian (Judithian) time.

The Scincidae are represented in the assemblage by two genera: first, *Penemabuya* shows a strong tendency in jaw construction and tooth morphology toward the Recent *Mabuya* group (which at present has a nearly worldwide distribution), and may represent an early Campanian precursor of it. Second, *Aocnodromeus* is characterized by having wrinkled enamel on the tooth crowns. The tooth morphology of this lizard indicates affinity with the Scincidae, but a robust subdental shelf and a strong mandibular symphysis are equally indicative of cordylid affinities.

Anguimorpha.—Both Xenosauridae and Anguidae are recorded by materials identified as "genus and species undetermined." However, both jugals and maxillaries referred to the Xenosauridae are clearly distinguishable from those of *Exostinus,* indicating that the Milk River record may represent a new genus and species. The Anguidae are represented by dentary materials that clearly show synapomorphic character states for the family, especially formation of the dorsal and anterior border of the anterior inferior alveolar foramen by the dentary (Estes, 1964; Estes et al., 1988). Previous to this study, an uncertain record of the Anguidae was reported from the Comanchean Paluxy Formation, central Texas (Winkler et al., 1990). However, as discussed elsewhere in this paper, this specimen is probably from a scincomorphan instead, as it has a robust subdental shelf and a sulcus dentalis. Ac-

cordingly, the Milk River specimens document the earliest undoubted record for the Anguidae.

The Necrosauridae* in this assemblage are recorded by an unnamed new genus and species, and fragmentary materials identified as "?*Parasaniwa* sp." The unnamed new taxon resembles the Lancian *Colpodontosaurus* in tooth form and dentary construction, and together with "?*Parasaniwa* sp.," the Milk River fossils document the earliest record for the family Necrosauridae*. On the other hand, advanced varanoids (Helodermatidae and Varanidae) are absent from the Aquilan assemblage.

Judithian (Mid-Campanian) Assemblage

Scincomorpha.—As shown in Figure 39, scincomorphans in the Judithian or mid-Campanian assemblage in western Canada are predominantly represented by teiids. Members of the Scincidae and ?Cordylidae also occur in the assemblage, while fossils of the Iguanidae*, known from both Aquilan and Lancian assemblages, are undiscovered in the Judithian. Contrary to the conclusions of previous authors (Sahni, 1972; Armstrong-Ziegler, 1980; Sullivan, 1981; Estes, 1983*a*), Judithian teiids are taxonomically different from those of Lancian age (see Estes, 1964, 1983*a*; Estes et al., 1969), resembling in that respect the mammals, which have fewer than 10% of the species in common between Judithian and Lancian horizons (see Lillegraven and McKenna, 1986). The taxonomic diversity of the Teiidae indicates an important pre-Lancian diversification of the family, and hence, reflects a significant episode in the evolutionary history of teiids (Gao and Fox, 1991).

Anguimorpha.—Judithian anguimorphans are better documented than those in the Aquilan assemblage, and are represented by the Xenosauridae, Anguidae, Necrosauridae*, Helodermatidae, and Varanidae (Fig. 40). The evolutionarily important taxon *Odaxosaurus* (see Meszoely, 1970; Sullivan, 1982, 1986*a*, 1986*b*; Estes, 1983*a*) makes its earliest discovered occurrence in the Oldman Formation, and is represented by a new species, *Odaxosaurus priscus,* which closely resembles the Lancian *O. piger,* but differs from the latter in having fewer, less truncate, and barely striated teeth, and in having the ventral border of the intramandibular septum extending anteriorly to the midpoint of the tooth row. *Parasaniwa* (Necrosauridae*) is well documented in terms of a large number of individuals (some 80 specimens), and both Helodermatidae and Varanidae first appear in North America in the Judithian assemblage.

Following the Judithian diversification of several lizard groups, there is a gap in the fossil record during the late Campanian and early Maastrichtian in western Canada. The only lizard taxon known from deposits of this age (Edmontonian) in the study area is a teiid ("*Chamops* cf. [*C.*] *segnis*" of Sternberg, 1951; "?*Chamops* sp." in this paper) from the Wapiti Formation at the Kleskun Hills, northwestern Alberta (see Sternberg, 1951; and relevant discussion in this paper). The gap may partially result from the transgression of the Bearpaw Sea that covered large areas in Alberta and Saskatchewan (see, e.g., Caldwell et al., 1978), and more importantly from lack of discovery of microvertebrate fossils from the nonmarine deposits of this age in the study area.

Lancian (Late Maastrichtian) Assemblage

Lancian or late Maastrichtian lizards are known in western Canada from the Scollard Formation, central Alberta, and the Frenchman Formation, southwestern Saskatchewan. In taxonomic composition, this assemblage is generally similar to that from the Lance and Hell Creek formations of Wyoming and Montana, but it includes several new taxa, as well.

Iguania.—The Iguanidae* in this assemblage are represented by at least one (or more than one) species from the Frenchman Formation; these lizards have high-crowned, flared, tricuspid teeth, resembling those of the extant *Ctenosaura,* a terrestrial, herbivorous iguanine found in Mexico and Central America (Etheridge and de Queiroz, 1988; Mattison, 1989).

Scincomorpha.—Lancian Teiidae are diverse, and are represented by five genera, of which four (*Chamops, Leptochamops, Meniscognathus,* and *Haptosphenus*) are already known from the Lance and Hell Creek formations; one (*Stypodontosaurus*) is new, and so far known only from the Scollard Formation. The Scincidae are absent from the Lancian assemblage; this may indicate that the family underwent a decline in North America slightly earlier than the Teiidae. The Lancian assemblage also includes possible cordylids and two xantusiids (*Contogenys* and an unnamed new taxon), which are unknown from pre-Lancian horizons.

Anguimorpha.—The Lancian anguimorphans from the study area include five genera in four families: *Exostinus* (Xenosauridae), *Odaxosaurus* (Anguidae), *Colpodontosaurus* and *Parasaniwa* (Nec-

rosauridae*), and *Paraderma* (Helodermatidae). All of these genera have been known previously from the type Lance Formation (see Estes, 1964). The Varanidae are absent from the Lancian assemblage in western Canada.

General Discussion on the Evolution of Late Cretaceous Lizards in Western Canada

Iguania.—For iguanians, the currently known Cretaceous fossil record from western Canada (as well as from North America) consists exclusively of the Iguanidae* (sensu lato), while in East Asia the family was sympatric with the Agamidae* in its early evolution (e.g., Borsuk-Bialynicka and Alifanov, 1991; Gao and Hou, 1992, 1995). Lack of a Mesozoic fossil record of agamids in North America, in keeping with current distribution of the group, may indicate that the highly derived agamids had never been a major group in the New World, except for a poor Eocene record (e.g., Marsh, 1872; Gilmore, 1928; Hecht, 1959).

The two early iguanids from the Milk River Formation are both tricuspid in crown pattern, and this tooth morphology of the Aquilan iguanids provides fossil evidence supporting the interpretation of Etheridge and de Queiroz (1988), who treated the tricuspid crown pattern as a primitive condition within iguanids. Etheridge and de Queiroz (1988) hypothesized two independent trends affecting crown pattern in iguanid evolution: one that included reduction and loss of lateral cusps, and a second marked by increasing cuspidation and broadening and flaring of the crowns. With the newly discovered fossils from the Upper Cretaceous of western Canada, the second trend can be corroborated, because the oldest known iguanids from the Milk River Formation show the more generalized, tricuspid condition, while iguanids from the geologically much younger Frenchman Formation have flared crowns, with a much stronger separation of the lateral cusps from the prominent central cusp. On the other hand, the first trend, reduction and loss of cusps, is not documented at all in the fossil record of early iguanids as currently known.

Scincomorpha.—Within the suborder Scincomorpha, the family Teiidae has a much better fossil record than any of the other families. The family in terms of species diversity is obviously the most predominant group in the Late Cretaceous lizard fauna both in the study area and in nearby regions (Wyoming and Montana). However, the number of species within the family experienced a sharp decline at the end of the Cretaceous Period in North America, accompanying the major extinctions of terrestrial vertebrates through the K–T transition (see, e.g., Archibald and Bryant, 1990; Sheehan and Fastovsky, 1992). The family may have invaded South and Central America before the K–T transition, and once in South America the family underwent a Tertiary Neotropical radiation. The fossil evidence also indicates that the divergence of Teiinae and the Tupinambinae may have taken place no later than mid-Campanian, as the Judithian assemblage includes fossil genera of both groups: *Socognathus* shows tupinambine affinities, as it displays character states such as heterodonty and suppression of tooth replacement in adults; and *Leptochamops* is allied with the Teiinae, as Estes (1964) recognized.

Another scincomorphan family occurring in the Upper Cretaceous of western Canada is the Scincidae. In spite of the great diversity and wide geographical distribution of Recent skinks, the family is poorly represented in the fossil record. In North America, two genera, *Contogenys* and *Sauriscus,* were originally assigned to the Scincidae (Estes, 1964, 1969*b*); however, as discussed in the preceding section on Xantusiidae, the former genus may have xantusiid affinities, while the latter could well be a cordylid, not a scincid (Estes, 1983*a,* 1983*b*). Our study supplements the Mesozoic record for the Scincidae as recently established by Rowe et al. (1992) and Richter (1994).

Two other scincomorphan families, Cordylidae and Xantusiidae, may also be documented in the fossil record from western Canada (or nearby areas). The uncertain referrals to these families of the fossil taxa described in this paper are largely because of lack of knowledge of the osteomorphology and life history of the two groups. However, the newly discovered specimens described in this paper represent a beginning in the accumulation of fossil evidence for a better understanding of the evolutionary history of the two families.

Anguimorpha.—Five anguimorphan families (Xenosauridae, Anguidae, Necrosauridae*, Helodermatidae, and Varanidae) are well documented in the three fossil assemblages from western Canada. Xenosauridae first appear in the Aquilan assemblage, and also occur in the Judithian and Lancian assemblages. Although represented by fragmentary materials, this record certainly shows a trend in xenosaurid evolution involving widening and more extensive ornamentation of the jugal. The Anguidae have their earliest definite record in the Aquilan assemblage, although they are

represented by fragmentary specimens identified as "genus and species undetermined." The basal glyptosaurine anguid *Odaxosaurus* first occurs in the Judithian assemblage, and is documented there by a new species, which is close to the type species, *O. piger.* A comparison of the Judithian species with *O. piger* reveals some morphological changes in the evolution of *Odaxosaurus*; these include shortening of the intramandibular septum and freeing of its ventral border, thickening of the crown enamel, and more prominent striations. *Odaxosaurus* was originally founded on dentary materials (Gilmore, 1928), but later work with added maxillaries, frontals, and parietals has in some degree changed the diagnosis of the species and raised certain issues about the relationships of *Odaxosaurus* with glyptosaurine anguids (see, e.g., Gauthier, 1982; Estes, 1983*a*; Sullivan, 1986*a,* 1986*b*). Newly discovered maxillary and dentary specimens with osteoderms from Lancian horizons show that disarticulated skull elements (frontals and parietals) may have been incorrectly associated with the maxillary and dentaries previously. However, a taxonomic revision of *Odaxosaurus piger* needs further study of better preserved jaw materials with osteoderms.

The Necrosauridae*, an extinct family of primitive varanoid lizards, are represented in western Canada by *Parasaniwa, Colpodontosaurus,* and an unnamed new genus and species. *Parasaniwa* was probably a common North American necrosaurid having an extensive fossil record from the latest Cretaceous Lance Formation of Wyoming. Now it is known from the Scollard and Frenchman formations of the same age, and more importantly from the Judithian Oldman and (possibly) Aquilan Milk River formations. This predaceous lizard differs from *Colpodontosaurus* principally in having sharply pointed, trenchant teeth with basal infoldings, and in having a more prominent intramandibular septum. "?*Parasaniwa* sp." from the Milk River Formation is recognized on fragmentary dentaries with poorly preserved teeth; therefore, the tooth form and dentary morphology of this early necrosaurid are not yet clearly known, and its comparison with the congeneric form from the younger horizon is correspondingly limited. A Judithian new species of *Parasaniwa* is recognized (but unnamed owing to the difficulty in designating a holotype from currently known specimens), and it shows more primitive character states than the Lancian type species *P. wyomingensis.* A comparison of the two species reveals that two notable changes in *Parasaniwa* evolution are: 1) from a relatively straight condition, the dentary tooth-bearing border became more crescentic; and 2) the parietal foramen shifted anteriorly from a posterior position, coupled with more extensive fusion of the osteoderms on the dorsal surface of the parietal. Nonetheless, the basic tooth morphology (trenchant blade without serrations and simple basal infoldings) and the condition of the intramandibular septum (fused to the floor of the Meckelian canal) remained unchanged from Judithian to Lancian time.

The Helodermatidae occur in Alberta and Montana as early as Judithian time, and are well documented in Lancian deposits in Wyoming, Alberta, and Saskatchewan. Both Judithian and Lancian helodermatids retain primitive character states, such as a parietal foramen, and a relatively greater number of teeth than in Recent species. However, Judithian *Labrodioctes* was substantially larger than Lancian *Paraderma* and does not have anterior venom grooves on the dentary teeth; *Paraderma* does have anterior venom grooves and appears to have been slightly larger than extant *Heloderma.* These differences may suggest that a general trend in helodermatid evolution is the reduction of body size, accompanied by the development of the venom gland and grooves. Previous authors (Bogert and del Campo, 1956; Pregill et al., 1986) have suggested that the venom gland and grooves of helodermatids were initially developed in a feeding context, but have secondarily assumed a function in defense. The large body size and robust teeth of the Judithian *Labrodioctes* certainly suggest that it was a more active predator than the Recent helodermatids. Although the origin of the venom groove in varanoid lizards is still obscure (see Norell et al., 1992), it is possible that during the evolution of helodermatids, the venom gland and grooves were further developed late in the Late Cretaceous, associated with a change of feeding style and in compensation for loss in body-size advantage.

The Varanidae have been known from western Canada for many years, since Gilmore (1923, 1928) first referred UA 112 (a dorsal vertebra) to the Lacertilia and subsequently named *Palaeosaniwa canadensis.* However, there have been disagreements concerning the familial assignment of this species (McDowell and Bogert, 1954; Estes, 1964, 1983*a*; Hoffstetter, 1969) because the species has only been known with certainty from disarticulated vertebrae. Described in this paper for the first time, both maxillaries and dentaries of this species show microserrations on the cutting edge of the teeth, supporting

the referral of *P. canadensis* to the Varanidae. *Palaeosaniwa canadensis* marks the earliest appearance of the Varanidae in North America (Gilmore, 1928; Estes, 1983*a*), and may provide the earliest record of the family overall, depending on the actual age and relationships of *Telmasaurus* (Gilmore, 1943*a*) from the Gobi Desert.

CONCLUSIONS

1. Upper Cretaceous nonmarine deposits of western Canada have yielded fossil lizards representing some 40 species in more than 30 genera of ten families. Hundreds of specimens collected from the Milk River, Oldman, Frenchman, and Scollard formations reveal previously unknown aspects of the evolutionary history of the relevant lizard families during the last 18 Myr of the Cretaceous Period in western Canada.

2. According to the differences in geologic age and taxonomic composition, three fossil assemblages are recognizable: first, the Aquilan assemblage documents an early diversification of the Iguanidae*, Scincidae, Xenosauridae, Anguidae, and Necrosauridae*; whereas the Teiidae are poorly recorded. Second, the Judithian assemblage reflects a major adaptive radiation of the Teiidae, and documents the earliest occurrence of helodermatids and varanids in North America. Third, the Lancian assemblage is taxonomically similar to that previously known from the Lance and Hell Creek formations, but includes several new taxa unknown from the latter formations.

3. The paucity of the Edmontonian lizard fossil record (during late Campanian and early Maastrichtian) in the main study area is probably partially the result of the transgression of the Bearpaw Sea, and, more importantly, a general lack of discovery of microvertebrate fossils from Edmontonian horizons.

4. The new discovery of Late Cretaceous iguanids from western Canada is especially significant, as it documents the first Mesozoic record for the Iguanidae* in North America, and, coupled with other discoveries from Asia, challenges the South American origin hypothesis and argues for a possible Northern Hemisphere origin of the family. The fossil evidence from western Canada also demonstrates that one of the evolutionary trends for the Iguanidae* is from a generalized, primitive, tricuspid tooth form to an advanced, widely flared crown pattern.

5. Teiids are important components in the Late Cretaceous lizard fauna of North America. Current knowledge of the fossil record of the Teiidae indicates that the family had a major radiation in North America (probably also in East Asia) in mid-Campanian time; but may have disappeared from northern continents at the K–T transition, as previous authors have suggested. Probably also in Campanian time, some of the North American teiids dispersed to Central and South America, where they underwent a Cenozoic Neotropical radiation.

6. The Scincidae were well established in North America by Aquilan time, but may have never become as diverse as the Teiidae in the North American continent. Their absence in the Lancian assemblage may suggest that the group had declined in North America slightly earlier than the Teiidae. Both Cordylidae and Xantusiidae may have a Late Cretaceous record in North America, but their evolutionary history remains poorly known because of poor preservation of the specimens.

7. The Xenosauridae first appear in western Canada in the Aquilan assemblage, and are also recorded in the Judithian assemblage. Fossil evidence indicates that the jugal may have tended to widen and become more extensively ornamented during their early evolution. New specimens from the Lance and Hell Creek formations reveal new data for better understanding of the problematic taxon *Exostinus.*

8. The Anguidae are definitely present in the Milk River Formation in western Canada, whereas the record of "Anguidae?" from the Comanchean, Texas, is probably of a scincomorphan. New *Odaxosaurus* specimens from Judithian to Lancian horizons show an evolutionary increase in the striations on the tooth crowns and shortening of the intramandibular septum. The new materials also indicate that previous workers may have incorrectly associated Lancian frontals and parietals with the maxillaries and dentaries of *Odaxosaurus.*

9. Necrosauridae* first appear in Aquilan assemblages and are represented in the study area by *Parasaniwa, Colpodontosaurus,* and an unnamed new genus and species. In the evolution of *Parasaniwa,* the dentary becomes more slender and the tooth-bearing border tends to become more crescentic; while tooth form and the condition of the intramandibular septum show little change from Judithian to Lancian time.

10. Both the Helodermatidae and the Varanidae

are first known in the Judithian lizard assemblage from North America. For the Helodermatidae, a major evolutionary trend may have been the reduction of body size paralleling a change in feeding style. The development of venom grooves on the marginal teeth may have been a compensation for the loss of the advantage that large body size confers.

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LITERATURE CITED

Alifanov, V. R. 1989. The most ancient gecko (Lacertilia, Gekkonidae) from the Lower Cretaceous of Mongolia. Paleontological Journal (Moscow), 1989:124–126.

Allan, J. A., and J. L. Carr. 1946. Geology and coal occurrences of Wapiti–Cutbank area, Alberta. Research Council of Alberta Report, 48:1–43.

Archibald, J. D. 1982. A study of the Mammalia and geology across the Cretaceous–Tertiary boundary in Garfield County, Montana. University of California Publications in Geological Sciences, 122:1–286.

———. 1987*a*. Latest Cretaceous and early Tertiary mammalian biochronology/biostratigraphy in the Western Interior. Geological Society of America, Abstracts with Programs, 19:258.

———. 1987*b*. The Bugcreekian Land Mammal Age: A reassessment. Journal of Vertebrate Paleontology, 7:10A, Supplement to No. 3: Abstracts of Papers, 47th Annual Meeting, Society of Vertebrate Paleontology, The University of Arizona, Tucson, Arizona.

———. 1994. Metataxon concepts and assessing possible ancestry using phylogenetic systematics. Systematic Biology, 43:27–40.

Archibald, J. D., and L. J. Bryant. 1990. Differential Cretaceous/Tertiary extinctions of nonmarine vertebrates; evidence from northeastern Montana. Pp. 549–562, *in* Global Catastrophes in Earth History; An Interdisciplinary Conference on Impacts, Volcanism, and Mass Mortality (V. L. Sharpton and P. D. Ward, eds.). Geological Society of America, Special Paper 247.

Armstrong-Ziegler, J. G. 1978. An aniliid snake and associated vertebrates from the Campanian of New Mexico. Journal of Paleontology, 52:480–483.

———. 1980. Amphibia and Reptilia from the Campanian of New Mexico. Fieldiana Geology, 4:1–39.

Astibia, H., E. Buffetaut, A. D. Buscalioni, H. Cappetta, C. Corral, R. Estes, F. Garcia-Garmilla, J. J. Jaeger, E. Jimenez-Fuentes, J. Le Loeuff, J. M. Mazin, X. Orue-Etxebarria, J. Pereda-Suberbiola, J. E. Powell, J. C. Rage, J. Rodriguez-Lazaro, J. L. Sanz, and H. Tong. 1990. The fossil vertebrates from Lano (Basque Country, Spain); New evidence on the composition and affinities of the Late Cretaceous continental faunas of Europe. Terra Nova, 2:460–466.

Barghusen, H. R., and J. A. Hopson. 1979. The endoskeleton: The comparative anatomy of the skull and the visceral skeleton. Pp. 265–326, *in* Hyman's Comparative Vertebrate Anatomy (M. Wake, ed.). The University of Chicago Press, Chicago, Illinois.

Benton, M. J. 1983. The Triassic reptile *Hyperodapedon* from Elgin: Functional morphology and relationships. Philosophical Transactions of the Royal Society, Series B, 302:605–717.

Blanc, C. P. 1982. Biogeographical aspects of the distribution of Malagasy iguanids and their implications. Pp. 38–45, *in* Iguanas of the World (G. M. Burghart and A. S. Rand, eds.). Noyes Publications, Park Ridge, New Jersey.

Bogert, C. 1964. Amphisbaenids are a taxonomic enigma. Natural History, 73:17–24.

Bogert, C., and R. del Campo. 1956. The Gila monster and its allies. Bulletin of the American Museum of Natural History, 109:1–238.

Böhme, W. 1981. Amphisbaenidae–Doppelschleichen. Pp. 275–276, *in* Handbuch der Reptilien und Amphibien Europas, Band 1 (W. Böhme, ed.). Akademische Verlagsgesellschaft, Wiesbaden, Germany.

Borsuk-Bialynicka, M. 1984. Anguimorphans and related lizards from the Late Cretaceous of the Gobi Desert, Mongolia. Palaeontologia Polonica, 46:5–105.

———. 1985. Carolinidae, a new family of xenosaurid-like lizards from the Upper Cretaceous of Mongolia. Acta Palaeontologica Polonica, 30:151–176.

———. 1986. On the diagnosis of the Xenosauridae (Anguimorpha). Pp. 213–218, *in* Studies in Herpetology (Z. Roček, ed.). Prague, Czechoslovakia.

———. 1988. *Globaura lenusta* gen. et sp. n. and *Eoxanta lacertifrons* gen. et sp. n.—non-teiid lacertoid from the Late Cretaceous of Mongolia. Acta Palaeontologica Polonica, 33: 211–248.

Borsuk-Bialynicka, M., and V. R. Alifanov. 1991. First Asiatic 'iguanid' lizards in the Late Cretaceous of Mongolia. Acta Palaeontologica Polonica, 36:325–342.

Boulenger, G. A. 1884. Synopsis of the families of existing Lacertilia. Annals and Magazine of Natural History, 14:117–122.

———. 1885. Catalogue of the lizards in the British Museum (Natural History), Volume II. Wheldon and Wesley Ltd, London, United Kingdom.

———. 1891. Notes on the osteology of *Heloderma horridum* and *H. suspectum,* with remarks on the systematic position of the Helodermatidae and on the vertebrae of the Lacertilia. Proceedings of the Zoological Society of London, 1891: 109–118.

———. 1892. Reptilia and Batrachia. Zoological Record, 29: Rept. 1-41.

Brinkman, D. B. 1990. Paleoecology of the Judith River Formation (Campanian) of Dinosaur Provincial Park, Alberta, Canada: Evidence from vertebrate microfossil localities. Palaeogeography, Palaeoclimatology, Palaeoecology, 78:37–54.

Brookins, D. G., and J. K. Rigby, Jr. 1987. Geochronologic and geochemical study of volcanic ashes from the Kirtland Shale (Cretaceous), San Juan Basin, New Mexico. Pp. 105–110, *in* The Cretaceous–Tertiary Boundary in the San Juan and Raton Basins, New Mexico and Colorado (J. E. Fassett and J. K. Rigby, Jr., eds.). Geological Society of America, Special Paper 209, Boulder, Colorado.

Brown, B. 1907. The Hell Creek beds of the Upper Cretaceous of Montana. Bulletin of the American Museum of Natural History, 23:823–845.

Bryant, L. T. 1985. Non-dinosaurian lower vertebrates across the Cretaceous–Tertiary boundary, northeastern Montana. Unpublished Ph.D. Dissert., University of California, Berkeley, California.

Caldwell, W. G. E., B. R. North, C. R. Stelck, and J. H. Wall. 1978. A foraminiferal zonal scheme for the Cretaceous System in the Interior Plains of Canada. Pp. 495–575, *in* Western and Arctic Canadian Biostratigraphy (C. R. Stelck and B. D. E. Chatterton, eds.). The Geological Association of Canada, Special Paper 18.

Camp, C. L. 1923. Classification of the lizards. Bulletin of the American Museum of Natural History, 48:289–481.

Carpenter, K. 1979. Vertebrate fauna of the Laramie Formation (Maestrichtian), Weld County, Colorado. The University of Wyoming, Contributions to Geology, 17:37–49.

Carroll, R. L. 1988. Vertebrate Paleontology and Evolution. W. H. Freeman and Co., New York, New York.

Chatterjee, S. K. 1974. A rhynchosaur from the Upper Triassic Maleri Formation of India. Philosophical Transactions of the Royal Society, Series B, 267:209–261.

Clemens, W. A., Jr. 1960. Stratigraphy of the type Lance Formation. Reports of the International Geological Congress, 21st Session, Part 5:7–13.

———. 1963. Fossil mammals of the type Lance Formation, Wyoming. Part I. Introduction and Multituberculata. University of California Publications in Geological Sciences, 48:1–105.

Clemens, W. A., Jr., and L. S. Russell. 1965. Mammalian fossils from the Upper Edmonton Formation. Pp. 41–52, *in* Vertebrate Paleontology in Alberta (C. R. Stelck, ed.). Department of Geology Bulletin 2, University of Alberta, Alberta, Canada.

Cobban, W. 1973. Significant ammonite finds in the uppermost Mancos Shale and overlying formations between Barker Dome, New Mexico and Grand Junction, Colorado. Memoir Four Corners Geological Society:148–153.

Conant, R. 1955. Saurian shell crusher. Nature Magazine (Washington), 48:85–86.

Cope, E. D. 1873. Synopsis of New Vertebrata from the Tertiary of Colorado, Obtained during the Summer of 1873. United States Government Printing Office, Washington, D. C.

———. 1884. The Vertebrata of the Tertiary formations of the West. Book I. Report of the United States Geological Survey of the Territories, 3:1–1009.

———. 1886. Thirteenth contribution to the herpetology of tropical America. Proceedings of the American Philosophical Society, Philadelphia, 23:271–287.

Cowles, R. B. 1930. The life history of *Varanus niloticus,* as observed in Natal, South Africa. Journal of Entomology and Zoology, 22:1–31.

Cracraft, J. 1973. Vertebrate evolution and biogeography in the Old World tropics. Pp. 373–393, *in* Implications of Continental Drift to the Earth Sciences (D. H. Tarling and S. K. Runcorn, eds.). Academic Press, New York, New York.

Crockford, M. B. B., and W. H. A. Clow. 1965. Upper Cretaceous formations of the Cypress Hills–Milk River area, southeastern Alberta and southwestern Saskatchewan. Pp. 184–197, *in* Cypress Hills Plateau, Alberta and Saskatchewan (R. L. Zell, ed.). Fifteenth Annual Field Conference of Alberta Society of Petroleum Geology, Guidebook.

Currie, P. J. 1986. Dinosaur fauna. Pp. 17–23, *in* Dinosaur Systematics Symposium, Field Trip Guidebook to Dinosaur Provincial Park (B. G. Naylor, ed.). Tyrrell Museum of Palaeontology, Drumheller, Alberta, Canada.

———. 1987. Bird-like characteristics of the jaws and teeth of troodontid theropods (Dinosauria, Saurischia). Journal of Vertebrate Paleontology, 7:72–81.

Darlington, P. J., Jr. 1957. Zoogeography: The Geographical Distribution of Animals. John Wiley and Sons, Inc., New York, New York.

Dawson, G. M. 1881. Report on an exploration from Port Simpson on the Pacific Coast to Edmonton on the Saskatchewan, embracing a portion of the northern part of British Columbia and the Peace River Country. Canada Geological Natural History Survey, Report of Progress 1879–1880, Part B:1–177.

de Muizon, C., M. Gayet, A. Lavenu, L. Marshall, B. Sigé, and C. Villaroel. 1983. Late Cretaceous vertebrates, including mammals, from Tiupampa, southcentral Bolivia. Geobios, 16:747–753.

Denton, R. K., Jr., and R. C. O'Neill. 1995. *Prototeius stageri,* gen. et sp. nov., a new teiid lizard from the Upper Cretaceous Marshalltown Formation of New Jersey, with a preliminary phylogenetic revision of the Teiidae. Journal of Vertebrate Paleontoloy, 15:235–253.

Denton, R. K., Jr., R. C. O'Neill, B. S. Grandstaff, and D. C. Parris. 1991. Earliest record of an advanced glyptosaurine lizard from the Late Cretaceous (Campanian) of New Jersey. Journal of Vertebrate Paleontology, 11:25A, Supplement to No. 3: Abstracts of Papers, 51st Annual Meeting, Society of Vertebrate Paleontology, San Diego State Uni-

versity and San Diego Natural History Museum, San Diego, California.

Dodson, P. 1983. A faunal review of the Judith River (Oldman) Formation, Dinosaur Provincial Park, Alberta. Mosasaur, 1: 89–118.

———. 1987. Microfaunal studies of dinosaur paleoecology, Judith River Formation of southern Alberta. Pp. 70–75, *in* Fourth Symposium of Mesozoic Terrestrial Ecosystems, Short Papers (P. J. Currie and E. H. Koster, eds.). Occasional Paper of the Tyrrell Museum of Palaeontology 3.

Dodson, P., and P. J. Currie. 1990. Neoceratopsia. Pp. 593–618, *in* The Dinosauria (D. B. Weishampel, P. Dodson, and H. Osmólska, eds.). University of California Press, Berkeley and Los Angeles, California.

Dorf, E. 1942. Upper Cretaceous floras of the Rocky Mountain region, II: Flora of the Lance Formation at its type locality, Niobrara County, Wyoming. Carnegie Institution of Washington Publications, 508:1–168.

Dott, R. H., Jr., and R. L. Batten. 1988. Evolution of the Earth. McGraw-Hill Book Co., New York, New York.

Dowling, D. B. 1917. The southern plains of Alberta. Geological Survey of Canada, Memoir, 93:1–200.

du Bois, E. P. 1943. The osteology of the skull of *Cnemidophorus*. American Midland Naturalist, 30:510–517.

Dunn, E. R. 1936. Notes on American mabuyas. Proceedings of the Academy of Natural Sciences of Philadelphia, 87: 533–557.

Eaton, J. G. 1993. Therian mammals from the Cenomanian (Upper Cretaceous) Dakota Formation, southwestern Utah. Journal of Vertebrate Paleontology, 13:105–124.

Eberth, D. A. (ed.). 1987. Palaeoecology of the Upper Cretaceous Judith River Formation at Dinosaur Provincial Park, Alberta, Canada—Fourth Symposium on Mesozoic Terrestrial Ecosystems, Field Trip "A." Occasional Papers of the Tyrrell Museum of Palaeontology, 1:1–33.

———. 1990*a*. Tectonic, sedimentologic and paleontologic significance of a disconformity in the upper Judith River Formation (Campanian) of south-central Alberta. Abstracts of Papers, 13th International Sedimentological Congress, Nottingham, England, Sediments, 1990:150.

———. 1990*b*. Stratigraphy and sedimentology of vertebrate microfossil sites in the uppermost Judith River Formation (Campanian), Dinosaur Provincial Park, Alberta, Canada. Palaeogeography, Palaeoclimatology, Palaeoecology, 78:1–36.

Eberth, D. A., and D. A. Hamblin. 1993. Tectonic, stratigraphic, and sedimentologic significance of a regional disconformity in the upper Judith River Group (Belly River wedge) of southern Alberta, Saskatchewan, and northern Montana. Canadian Journal of Earth Sciences, 30:174–200.

Edmund, A. G. 1969. Dentition. Pp. 117–200, *in* Biology of the Reptilia, Volume 1 (C. Gans, A. d'A. Bellairs, and T. S. Parsons, eds.). Academic Press, London, United Kingdom, and New York, New York.

Estes, R. 1964. Fossil vertebrates from the Late Cretaceous Lance Formation eastern Wyoming. University of California Publications in Geological Sciences, 49:1–180.

———. 1965. Notes on some Paleocene lizards. Copeia, 1965: 104–106.

———. 1969*a*. Relationships of two Cretaceous lizards (Sauria, Teiidae). Breviora, 317:1–8.

———. 1969*b*. A scincid lizard from the Cretaceous and Paleocene of Montana. Breviora, 331:1–9.

———. 1975. Lower vertebrates from the Fort Union Formation, late Paleocene, Big Horn Basin, Wyoming. Herpetologica, 31:365–385.

———. 1976. Middle Paleocene lower vertebrates from the Tongue River Formation, southeastern Montana. Journal of Paleontology, 50:500–520.

———. 1983*a*. Sauria Terrestria, Amphisbaenia. Handbuch der Paläoherpetologie, Part 10A, Gustav Fisher Verlag, Stuttgart, Germany.

———. 1983*b*. The fossil record and early distribution of lizards. Pp. 365–398, *in* Advances in Herpetology and Evolutionary Biology: Essays in Honor of Ernest E. Williams (A. G. J. Rhodin and K. Kiyata, eds.). Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts.

———. 1985. Reevaluation of North American Late Cretaceous amphibians and reptiles. Geological Society of America, Abstracts with Programs, 17:217.

———. 1987. Lucas and Zidek on taxonomic syntax. Journal of Vertebrate Paleontology, 7:101.

———. 1991. Recent perspectives on phylogenetic relationships among reptiles. Pp. 225–254, *in* Symposium on the Evolution of Terrestrial Vertebrates: Proceedings of the International Symposium on Evolution of Terrestrial Vertebrates, Naples (G. Ghiara, ed.). Selected Symposia and Monographs 4, Collana Unione Zoologica Italiana, Modena, Italy.

Estes, R., and A. Báez. 1985. Herpetofaunas of North and South America during the Late Cretaceous and Cenozoic: Evidence for interchange? Pp. 139–197, *in* The Great American Biotic Interchange (F. G. Stehli and S. D. Webb, eds.). Plenum Press, New York, New York, and London, United Kingdom.

Estes, R., and P. Berberian. 1970. Paleoecology of a Late Cretaceous vertebrate community from Montana. Breviora, 343: 1–35.

Estes, R., P. Berberian, and C. Meszoely. 1969. Lower vertebrates from the Late Cretaceous Hell Creek Formation, McCone County, Montana. Breviora, 337:1–31.

Estes, R., K. de Queiroz, and J. Gauthier. 1988. Phylogenetic relationships within Squamata. Pp. 119–281, *in* Phylogenetic Relationships of the Lizard Families (R. Estes and G. Pregill, eds.). Stanford University Press, Stanford, California.

Estes, R., and L. I. Price. 1973. Iguanid lizard from the Upper Cretaceous of Brazil. Science, 180:748–751.

Estes, R., and E. E. Williams. 1984. Ontogenetic variation in the molariform teeth of lizards. Journal of Vertebrate Paleontology, 4:96–107.

Etheridge, R. 1964. The skeletal morphology and systematic relationships of sceloporine lizards. Copeia, 1964:610–631.

Etheridge, R., and K. de Queiroz. 1988. A phylogeny of Iguanidae. Pp. 283–367, *in* Phylogenetic Relationships of the Lizard Families (R. Estes and G. Pregill, eds.). Stanford University Press, Stanford, California.

Evans, S. E. 1988. The early history and relationships of the Diapsida. Pp. 221–260, *in* The Phylogeny and Classification of the Tetrapods, Volume 1: Amphibians, Reptiles, Birds (M. J. Benton, ed.). The Systematics Association, Special Volume No. 35A, Clarendon Press, Oxford, United Kingdom.

———. 1990. The skull of *Cteniogenys,* a choristodere (Reptilia: Archosauromorpha) from the Middle Jurassic of Oxfordshire. Zoological Journal of the Linnean Society, 99: 205–237.

FASSETT, J. E. 1987. The ages of the continental, Upper Cretaceous, Fruitland Formation and Kirtland Shale based on a projection of ammonite zones from the Lewis Shale, San Juan Basin, New Mexico and Colorado. Pp. 5–16, *in* The Cretaceous–Tertiary Boundary in the San Juan and Raton Basins, New Mexico and Colorado (J. E. Fassett and J. K. Rigby, Jr., eds.). Geological Society of America, Special Paper 209, Boulder, Colorado.

FASSETT, J., AND J. HINDS. 1971. Geology and fuel resources of the Fruitland Formation and Kirtland Shale of the San Juan Basin, New Mexico and Colorado. United States Geological Survey Professional Paper, 676:1–76.

FASTOVSKY, D. E. 1987. Paleoenvironments of vertebrate-bearing strata during the Cretaceous–Paleogene transition, eastern Montana and western North Dakota. Palaios, 2:282–295.

FISHER, D. C. 1981. Crocodilian scatology, microvertebrate concentrations, and enamel-less teeth. Paleobiology, 7:262–275.

FOLINSBEE, R. E., H. BAADSGAARD, G. L. CUMMING, J. NASCIMBENE, AND M. SHAFIQULLAH. 1965. Late Cretaceous radiometric dates from the Cypress Hills of western Canada. Pp. 162–174, *in* Cypress Hills Plateau, Alberta and Saskatchewan (R. L. Zell, ed.). Fifteenth Annual Field Conference of Alberta Society of Petroleum Geology, Guidebook.

FOX, R. C. 1968. Early Campanian (Late Cretaceous) mammals from Alberta, Canada. Nature, 220:1046.

———. 1969. Studies of Late Cretaceous vertebrates III—A triconodont mammal from Alberta. Canadian Journal of Zoology, 47:1253–1256.

———. 1970. Eutherian mammal from the early Campanian (Late Cretaceous) of Alberta, Canada. Nature, 227:630–631.

———. 1971. Marsupial mammals from the early Campanian Milk River Formation, Alberta, Canada. Pp. 145–164, *in* Early Mammals (D. M. Kermack and K. A. Kermack, eds.). Supplement 1, Zoological Journal of the Linnean Society, Volume 50.

———. 1972*a*. A primitive therian mammal from the Upper Cretaceous of Alberta. Canadian Journal of Earth Sciences, 9:1479–1494.

———. 1972*b*. An Upper Cretaceous symmetrodont mammal from Alberta, Canada. Nature, 239:170–171.

———. 1976. Upper Cretaceous and Paleocene vertebrate paleontology in Alberta. Annual Meeting of the Geological Association of Canada/Mineralogical Association of Canada, A-6 Field Trip Guidebook.

———. 1978. Upper Cretaceous terrestrial vertebrate stratigraphy of the Gobi Desert (Mongolian People's Republic) and western North America. Pp. 577–594, *in* Western and Arctic Canadian Biostratigraphy (C. R. Stelck and B. D. E. Chatterton, eds.). The Geological Association of Canada, Special Paper 18.

———. 1984. *Paranyctoides maleficus* (new species), an early eutherian mammal from the Cretaceous of Alberta. Pp. 9–20, *in* Papers in Vertebrate Paleontology Honoring Robert Warren Wilson (R. M. Mengel, ed.). Carnegie Museum of Natural History, Special Publication 9.

———. 1985. Upper molar structure in the Late Cretaceous symmetrodont *Symmetrodontoides* Fox, and a classification of the Symmetrodonta (Mammalia). Journal of Paleontology, 59:21–26.

———. 1989. The Wounded Knee local fauna and mammalian evolution near the Cretaceous–Tertiary boundary, Saskatchewan, Canada. Palaeontographica, Abteilung A, 208:11–59.

FOX, R. C., AND B. G. NAYLOR. 1982. A reconsideration of the relationships of the fossil amphibian *Albanerpeton*. Canadian Journal of Earth Sciences, 19:118–128.

FROST, D. R., AND R. ETHERIDGE. 1989. A phylogenetic analysis and taxonomy of iguanian lizards (Reptilia: Squamata). The University of Kansas Museum of Natural History, Miscellaneous Publication, 81:1–65.

FUNNELL, B. M. 1990. Global and European Cretaceous shorelines, stage by stage. Pp. 221–235, *in* Cretaceous Resources, Events and Rhythms (R. N. Ginsburg and B. Beaudoin, eds.). Kluwer Academic Publishers, Dordrecht, The Netherlands.

FURNIVAL, G. M. 1946. Cypress Lake map-area, Saskatchewan. Geological Survey of Canada, Memoir, 242:1–161.

GANS, C. 1958. Modifications of the head joint in acrodont amphisbaenids and their functional implications (abstract). Anatomical Record, 132:441.

———. 1978. The characteristics and affinities of the Amphisbaenia. Transactions of the Zoological Society of London, 34:347–416.

GAO, K. 1994. First discovery of Late Cretaceous cordylids (Squamata) from Madagascar. Journal of Vertebrate Paleontology, 14:26A, Supplement to No. 3: Abstracts of Papers, 54th Annual Meeting, Society of Vertebrate Paleontology, Burke Museum, University of Washington, Seattle, Washington.

GAO, K., AND R. C. FOX. 1991. New teiid lizards from the Upper Cretaceous Oldman Formation (Judithian) of southeastern Alberta, Canada, with a review of the Cretaceous record of teiids. Annals of Carnegie Museum, 60:145–162.

GAO, K., AND L. HOU. 1992. Fossil lizards from the Upper Cretaceous Djadochta Formation, the Gobi Desert of China. Journal of Vertebrate Paleontology, 12:29A, Supplement to No. 3: Abstracts of Papers, 52nd Annual Meeting, Society of Vertebrate Paleontology, Royal Ontario Museum, Toronto, Ontario, Canada.

———. 1995. Iguanians from the Upper Cretaceous Djadochta Formation, Gobi Desert, China. Journal of Vertebrate Paleontology, 15:57–78.

GAUTHIER, J. 1982. Fossil Xenosauridae and Anguidae from the lower Eocene Wasatch Formation, southcentral Wyoming, and a revision of the Anguioidea. The University of Wyoming, Contributions to Geology, 21:7–54.

GAUTHIER, J., R. ESTES, AND K. DE QUEIROZ. 1988. A phylogenetic analysis of Lepidosauromorpha. Pp. 15–98, *in* Phylogenetic Relationships of the Lizard Families (R. Estes and G. Pregill, eds.). Stanford University Press, Stanford, California.

GIBSON, D. S. 1977. Upper Cretaceous and Tertiary coal-bearing strata in the Drumheller–Ardley region, Red Deer River Valley, Alberta. Geological Survey of Canada, Paper 76-35:1–41.

GILMORE, C. W. 1922. A new description of *Saniwa ensidens* Leidy, an extinct varanid lizard from Wyoming. Proceedings of the United States National Museum, 60:1–28.

———. 1923. A new species of *Corythosaurus*, with notes on other Belly River Dinosauria. Canadian Field Naturalist, 37: 46–52.

———. 1926. On a nearly complete lizard skull from the Oligocene of Nebraska. Kansas University Science Bulletin, 16: 229–233.

———. 1928. Fossil lizards of North America. National Academy of Sciences, Memoir, 22:1–201.

———. 1932. A new fossil lizard from the Belly River For-

mation of Alberta. Transactions of the Royal Society of Canada, Series 3, 26:117–119.

———. 1940. New fossil lizards from the Upper Cretaceous of Utah. Smithsonian Miscellaneous Collections, 99:1–3.

———. 1942*a*. Paleocene faunas of the Polecat Bench Formation, Park County, Wyoming—Part II. Lizards. Proceedings of the American Philosophical Society, Philadelphia, 85: 159–167.

———. 1942*b*. Osteology of *Polyglyphanodon*, an Upper Cretaceous lizard from Utah. Proceedings of the United States National Museum, 92:229–265.

———. 1943*a*. Fossil lizards of Mongolia. Bulletin of the American Museum of Natural History, 81:361–384.

———. 1943*b*. Osteology of Upper Cretaceous lizards from Utah, with a description of a new species. Proceedings of the United States National Museum, 93:209–214.

Golz, D., and J. A. Lillegraven. 1977. Summary of known occurrences of terrestrial vertebrates from Eocene strata of southern California. The University of Wyoming, Contributions to Geology, 15:43–65.

Goodrich, E. S. 1930. Studies on the Structure and Development of Vertebrates. Constable and Company Ltd., London, United Kingdom.

Gorman, G. C. 1970. Chromosomes and the systematics of the family Teiidae (Sauria, Reptilia). Copeia, 1970:230–245.

Greene, H. 1982. Dietary and phenotypic diversity in lizards: Why are some organisms specialized? Pp. 107–128, *in* Environmental Adaptation and Evolution (D. Mossakowski and G. Roth, eds.). Gustav Fischer Verlag, Stuttgart, Germany, and New York, New York.

Greer, A. E. 1970. A subfamilial classification of scincid lizards. Bulletin of the Museum of Comparative Zoology, Harvard University, 139:151–184.

———. 1991. Tooth number in the scincid lizard genus *Ctenotus*. Journal of Herpetology, 25:473–477.

Harland, W. B., R. L. Armstrong, A. V. Cox, L. E. Craig, A. G. Smith, and D. G. Smith. 1990. A Geologic Time Scale 1989. Cambridge University Press, Cambridge, United Kingdom.

Harris, V. A. 1963. The Anatomy of the Rainbow Lizard. Hutchinson and Co., Ltd., London, United Kingdom.

———. 1964. The Life of the Rainbow Lizard. Hutchinson and Co., Ltd., London, United Kingdom.

Hatcher, J. B. 1896. Some localities for Laramie mammals and horned dinosaurs. American Naturalist, 30:112–120.

Hay, O. P. 1902. Bibliography and catalogue of the fossil Vertebrata of North America. Bulletin of the United States Geological Survey, 179:1–868.

Hecht, M. 1951. Fossil lizards of the West Indian genus *Aristelliger* (Gekkonidae). American Museum Novitates, 1538: 1–33.

———. 1956. A new xantusiid lizard from the Eocene of Wyoming. American Museum Novitates, 1774:1–8.

———. 1959. Amphibians and reptiles. Pp. 130–146, *in* The Geology and Paleontology of the Elk Mountain and Tabernacle Butte Area, Wyoming (P. O. McGrew, ed.). Bulletin of the American Museum of Natural History, 117:117–176.

Hoffstetter, R. 1943. Varanidae et Necrosauridae fossiles. Bulletin du Muséum National d'histoire Naturelle, Paris, 15: 134–141.

———. 1957. Un Saurien helodermatidé (*Eurheloderma gallicum* nov. gen. et sp.) dans la faunc fossile des phosphorites du Quercy. Bulletin de la Société Géologique de France, 7: 775–786.

———. 1969. Présence de Varanidae (Reptilia, Sauria) dans le Miocène de Catalogne—Considérations sur l'histoire de la famille. Bulletin du Muséum National d'histoire Naturelle, Paris, 40:1051–1064.

Hoffstetter, R., and J. P. Gasc. 1967. Observations sur le squelette cervical et spécialement sur les hypapophyses des sauriens varanoides actuels et fossiles. Bulletin du Muséum National d'histoire Naturelle, 39:1028–1043.

———. 1969. Vertebrae and ribs of modern reptiles. Pp. 201–310, *in* Biology of the Reptilia, Volume 1 (C. Gans, A. d'A. Bellairs, and T. S. Parsons, eds.). Academic Press, London, United Kingdom, and New York, New York.

Hotton, N. 1955. A survey of adaptive relationships of dentition to diet in the North American Iguanidae. American Midland Naturalist, 53:88–114.

ICZN. 1985. International Code of Zoological Nomenclature Adopted by the XX General Assembly of the International Union of Biological Sciences. International Trust for Zoological Nomenclature and University of California Press, London, United Kingdom, and Berkeley, California.

Irish, E. J. W. 1970. The Edmonton Group of south-central Alberta. Bulletin of Canadian Petroleum Geology, 18:125–155.

Jerzykiewicz, T., and D. A. Russell. 1991. Late Mesozoic stratigraphy and vertebrates of the Gobi Basin. Cretaceous Research, 12:345–377.

Johnston, P. A., and R. C. Fox. 1984. Paleocene and Late Cretaceous mammals from Saskatchewan, Canada. Palaeontographica, Abteilung A, 186:163–222.

Kochva, E. 1974. Glandes spécialisées de la machoire inférieure chez les Anguimorphes. Pp. 281–286, *in* Recherches Biologiques Contemporaines (L. Arvy, ed.). Imprimerie Vagner, Nancy, France.

Koster, E. H., P. J. Currie, D. Eberth, D. Brinkman, P. Johnston, and D. Braman. 1987. Sedimentology and palaeontology of the Upper Cretaceous Judith River/Bearpaw formations at Dinosaur Provincial Park, Alberta. Tyrrell Museum of Palaeontology, Drumheller, Alberta, Canada.

Langston, W., Jr. 1965. Pre-Cenozoic vertebrate paleontology in Alberta: Its past and future. Pp. 9–13, *in* Vertebrate Paleontology in Alberta (C. R. Stelck, ed.). Department of Geology Bulletin 2, University of Alberta, Edmonton, Alberta, Canada.

Laurin, M. 1991. The osteology of a Lower Permian eosuchian from Texas and a review of diapsid phylogeny. Zoological Journal of the Linnean Society (1991), 101:59–95.

Lécuru, S. 1969. Étude morphologique de l'humerus des lacertiliens. Annales des Sciences Naturelles, Zoologie, 11: 515–558.

Leidy, J. 1870. (Descriptions of *Emys jeansei, E. haydeni, Baena arenosa,* and *Saniwa ensidens*). Proceedings of the Academy of Natural Sciences of Philadelphia, 1870:123–124.

Lerbekmo, J. F. 1987. Magnetostratigraphic restrictions on the age of the Frenchman Formation and the magnitude of the sub-Frenchman disconformity in southwest Saskatchewan. Bulletin of Canadian Petroleum Geology, 35:454–459.

———. 1989. The stratigraphic positon of the 33-33R (Campanian) polarity chron boundary in southeastern Alberta. Bulletin of Canadian Petroleum Geology, 37:43–47.

Lerbekmo, J. F., and K. C. Coulter. 1985. Late Cretaceous to early Tertiary magnetostratigraphy of a continental se-

quence: Red Deer Valley, Alberta, Canada. Canadian Journal of Earth Sciences, 22:567–583.

LI, J. 1985. A new lizard from Late Jurassic of Subei, Gansu. Vertebrata PalAsiatica, 23:13–18.

LILLEGRAVEN, J. A. 1969. Latest Cretaceous mammals of upper part of Edmonton Formation of Alberta, Canada, and review of marsupial–placental dichotomy in mammalian evolution. The University of Kansas Paleontological Contributions, Article 50 (Vertebrata 12):1–122.

———. 1991. Stratigraphic placement of the Santonian–Campanian boundary (Upper Cretaceous) in the North American Gulf Coastal Plain and Western Interior, with implications to global geochronology. Cretaceous Research, 12:115–136.

LILLEGRAVEN, J. A., AND M. C. MCKENNA. 1986. Fossil mammals from the "Mesaverde" Formation (Late Cretaceous, Judithian) of the Big Horn and Wind River basins, with definitions of the Late Cretaceous Land Mammal "Ages." American Museum Novitates, 2840:1–68.

LILLEGRAVEN, J. A., AND L. M. OSTRESH, JR. 1990. Late Cretaceous (earliest Campanian/Maastrichtian) evolution of western shorelines of the North American Western Interior Seaway in relation to known mammalian faunas. Pp. 1–30, *in* Dawn of the Age of Mammals in the Northern Part of the Rocky Mountain Interior, North America (T. M. Bown and K. D. Rose, eds.). Geological Society of America, Special Paper 243.

LONNBERG, E. 1903. On the adaptation to a molluscivorous diet in *Varanus niloticus*. Arkiv för Zoologi, 1:65–82.

LUCAS, S. G. 1986. Proper syntax when using aff. and cf. in taxonomic statements. Journal of Vertebrate Paleontology, 6:202.

LUCAS, S. G., N. J. MATEER, A. P. HUNT, AND F. M. O'NEILL. 1987. Dinosaurs, the age of the Fruitland and Kirtland formations, and the Cretaceous–Tertiary boundary in the San Juan Basin, New Mexico and Colorado. Pp. 35–50, *in* The Cretaceous–Tertiary Boundary in San Juan and Raton Basins, New Mexico and Colorado (J. E. Fassett and J. K. Rigby, Jr., eds.). Geological Society of America, Special Paper 209, Boulder, Colorado.

MACLEAN, W. P. 1974. Feeding and locomotion mechanisms of teiid lizards; Functional morphology and evolution. Papeis Avulsos Zoologia, 27:179–213.

MALAN, M. E. 1963. The dentitions of the South American Rhynchocephalia and their bearing on the origin of the rhynchosaurs. South African Journal of Science, 59:214–220.

MARSH, O. C. 1872. Preliminary description of new Tertiary reptiles. American Journal of Science, Series 3, 4:298–309.

———. 1889. Discovery of Cretaceous Mammalia. American Journal of Science, Series 3, 38:81–92.

———. 1892. Notice of new reptiles from the Laramie Formation. American Journal of Science, Series 3, 43:449–453.

MATTISON, C. 1989. Lizards of the World. Facts on File, Inc., New York, New York.

MAYR, E., AND P. D. ASHLOCK. 1991. Principles of Systematic Zoology. McGraw-Hill, Inc., New York, New York.

MCDOWELL, S., AND C. M. BOGERT. 1954. The systematic position of *Lanthanotus* and the affinities of the anguinomorphan lizards. Bulletin of the American Museum of Natural History, 105:1–142.

MCGOWAN, G., AND S. E. EVANS. 1995. Albanerpetontid amphibians from the Cretaceous of Spain. Nature, 373:143–145.

MCKENNA, M. C. 1960. Fossil Mammalia from the early Wasatchian Four Mile fauna, Eocene of northwest Colorado. University of California Publications in Geological Sciences, 37:1–130.

MCLEAN, J. R. 1971. Stratigraphy of the Upper Cretaceous Judith River Formation in the Canadian Great Plains. Saskatchewan Research Council, Geological Division Report, 11:1–96.

———. 1977. Lithostratigraphic nomenclature of the Upper Cretaceous Judith River Formation in southern Alberta: Philosophy and practice. Bulletin of Canadian Petroleum Geology, 25:1105–1114.

MESZOELY, C. 1970. North American fossil anguid lizards. Bulletin of the Museum of Comparative Zoology, Harvard University, 139:87–149.

MESZOELY, C., R. ESTES, AND H. HAUBOLD. 1978. Eocene anguid lizards from Europe and a revision of the genus *Xestops*. Herpetologica, 34:156–166.

MOFFAT, L. 1973. The concept of primitiveness and its bearing on the phylogenetic classification of the Gekkota. Proceedings of the Linnean Society of New South Wales, 97:275–301.

MONES, A. 1989. Nomen dubium vs. nomen vanum. Journal of Vertebrate Paleontology, 9:232–234.

MURRY, P. A., D. A. WINKLER, AND L. L. JACOBS. 1989. Small tetrapods from the Comanchean (Early Cretaceous) of central Texas. Journal of Vertebrate Paleontology, 9:33A–34A, Supplement to No. 3: Abstracts of Papers, 49th Annual Meeting, Society of Vertebrate Paleontology, University of Texas, Austin, Texas.

NESSOV, L. A. 1985. Rare bony fishes, terrestrial lizards and mammals from the lagoonal zone of the littoral lowlands of the Cretaceous of the Kyzylkumy. Year-Book of All-Union Palaeontological Society, Leningrad, 28:199-219 (in Russian).

———. 1988. Late Mesozoic amphibians and lizards of Soviet Middle Asia. Acta Zoologica Cracoviensia, 31:475–486.

NICHOLLS, E. L., AND A. P. RUSSELL. 1990. Paleobiogeography of the Cretaceous Western Interior Seaway of North America: The vertebrate evidence. Palaeogeography, Palaeoclimatology, Palaeoecology, 79:149–169.

NOPCSA, F. 1908. Zur Kenntniss der Fossilen Eidechsen. Beiträge zur Paläontologie und Geologie österreich–Ungarns und des Orients, 21:33–62.

NORELL, M. A., M. C. MCKENNA, AND M. J. NOVACEK. 1992. *Estesia mongoliensis*, a new fossil varanoid from the Late Cretaceous Barun Goyot Formation of Mongolia. American Museum Novitates, 3045:1–24.

NORTHCUTT, R. G. 1978. Forebrain and midbrain organization in lizards and its phylogenetic significance. Pp. 11–64, *in* Behavior and Neurology of Lizards (N. Greenberg and P. D. MacLean, eds.). United States Department of Health, Education and Welfare, Publication No. 77–491.

———. 1979. The comparative anatomy of the nervous system and the sense organs. Pp. 615–769, *in* Hyman's Comparative Vertebrate Anatomy (M. H. Wake, ed.). The University of Chicago Press, Chicago, Illinois.

ODERMATT, C. 1940. Beiträge zur Kenntnis des Gebisses von *Heloderma*. Vierteljahrsschrift der Naturforschenden Gesellschaft, Zürich, 85:98–141.

OLMO, E., AND G. ODIERNA. 1980. Chromosomal evolution and DNA of cordylid lizards. Herpetologica, 36:311–316.

OSMÓLSKA, H., AND R. BARSBOLD. 1990. Troodontidae. Pp. 259–268, *in* The Dinosauria (D. B. Weishampel, P. Dodson, and

H. Osmólska, eds.). University of California Press, Berkeley and Los Angeles, California.

Parris, D. C., and B. S. Grandstaff. 1989. Nonmarine microvertebrates of the Ellisdale local fauna: Campanian of New Jersey. Journal of Vertebrate Paleontology, 9:35A, Supplement to No. 3: Abstracts of Papers, 49th Annual Meeting, Society of Vertebrate Paleontology, The University of Texas, Austin, Texas.

Peters, J. A., R. Donoso-Barros, B. Orejas-Miranda, and P. E. Vanzolini. 1986. Catalogue of the Neotropical Squamata. Smithsonian Institution Press, Washington, D. C., and London, United Kingdom.

Pregill, G. K., J. A. Gauthier, and H. W. Greene. 1986. The evolution of helodermatid squamates, with description of a new taxon and an overview of Varanoidea. Transactions of the San Diego Society of Natural History, 21:167–202.

Presch, W. 1970. The evolution of macroteiid lizards: An osteological interpretation. Unpublished Ph.D. Dissert., University of Southern California, Los Angeles, California.

———. 1974*a*. Evolutionary relationships and biogeography of the macroteiid lizards (family Teiidae, subfamily Teiinae). Bulletin of the Southern California Academy of Science, 73: 23–32.

———. 1974*b*. A survey of the dentition of the macroteiid lizards (Teiidae: Lacertilia). Herpetologica, 30:344–349.

———. 1975. The evolution of limb reduction in the teiid lizard genus *Bachia*. Bulletin of the Southern California Academy of Science, 74:113–121.

———. 1983. The lizard family Teiidae: Is it a monophyletic group? Zoological Journal of the Linnean Society, 77:189–197.

Price, R. A., and E. W. Mountjoy. 1970. Geologic structure of the Canadian Rocky Mountains, between Bow and Athabasca Rivers: A progress report. Pp. 7–25, *in* Structure of the Southern Canadian Cordillera (J. O. Wheeler, ed.). The Geological Association of Canada, Special Paper 6.

Rage, J. C. 1991. Squamate reptiles from the early Paleocene of the Tiupampa area (Santa Lucia Formation), Bolivia. Revista Técnica de Yacimientos Petroliferos Fiscales Bolivianos, 12:503–508.

Rage, J. C., and M. Augé. 1993. Squamates from the Cainozoic of the western part of Europe: A review. Revue de Paléobiologie, volume spécial 7:199–216.

Rahmani, R. A., and J. F. Lerbekmo. 1975. Heavy-mineral analysis of Upper Cretaceous and Paleocene sandstones in Alberta and adjacent area of Saskatchewan. Pp. 607–632, *in* The Cretaceous System in the Western Interior of North America (W. G. E. Caldwell, ed.). The Geological Association of Canada, Special Paper 13.

Ray, C. E. 1965. Variation in the number of marginal tooth positions in three species of iguanid lizards. Breviora, 236: 1–15.

Richter, A. 1994. Lacertilia aus der Unteren Kreide um Uña und Galva (Spanien) und Anoual (Marokko). Berliner Geowissenschaftliche Abhandlungen, Reihe E, Band 14:1–138.

Rieppel, O. 1978. Tooth replacement in anguimorph lizards. Zoomorphologic, 91:77–90.

———. 1988. The classification of the Squamata. Pp. 261–293, *in* The Phylogeny and Classification of the Tetrapods, Volume 1: Amphibians, Reptiles, Birds (M. J. Benton, ed.). The Systematics Association, Special Volume No. 35A, Clarendon Press, Oxford, United Kingdom.

Rigby, J. K., Jr., and D. L. Wolberg. 1987. The therian mammalian fauna (Campanian) of Quarry 1, Fossil Forest study area, San Juan Basin, New Mexico. Pp. 51–79, *in* The Cretaceous/Tertiary Boundary in the San Juan and Raton Basins, New Mexico and Colorado (J. E. Fassett and J. K. Rigby, Jr., eds.). Geological Society of America, Special Paper 209, Boulder, Colorado.

Robinson, P. L. 1967. The evolution of the Lacertilia. Colloques Internationaux du Centre National de la Recherche Scientifique, 163:395–407.

Romer, A. S. 1956. Osteology of the Reptiles. The University of Chicago Press, Chicago, Illinois.

———. 1966. Vertebrate Paleontology. The University of Chicago Press, Chicago, Illinois.

Rowe, T., R. L. Cifelli, T. M. Lehman, and A. Weil. 1992. The Campanian Terlingua local fauna, with a summary of other vertebrates from the Aguja Formation, Trans-Pecos Texas. Journal of Vertebrate Paleontology, 12:472–493.

Ruibal, R. 1952. Revisionary studies of some South American Teiidae. Bulletin of the Museum of Comparative Zoology, Harvard University, 106:477–529.

Russell, D. A. 1969. A new specimen of *Stenonychosaurus* from the Oldman Formation (Cretaceous) of Alberta. Canadian Journal of Earth Sciences, 6:595–612.

———. 1989. An Odyssey in Time: The Dinosaurs of North America. University of Toronto Press, Toronto, Ontario, Canada.

Russell, L. S. 1935. Fauna of the upper Milk River beds, southern Alberta. Transactions of the Royal Society of Canada, Series 3, 29:115–128

———. 1964. Cretaceous non-marine faunas of northwestern North America. Contributions Royal Ontario Museum, Life Sciences, 6:1–24.

———. 1975. Mammalian faunal succession in the Cretaceous system of western North America. Pp. 137–161, *in* The Cretaceous System in the Western Interior of North America (W. G. E. Caldwell, ed.). The Geological Association of Canada, Special Paper 13.

Russell, L. S., and R. W. Landes. 1940. Geology of the southern Alberta Plains. Geological Survey of Canada, Memoir, 221:1–223.

Sahni, A. 1972. The vertebrate fauna of the Judith River Formation, Montana. Bulletin of the American Museum of Natural History, 147:321–412.

Saint-Girons, H. 1968. La morphologie comparée des glandes endocrines et la phylogenie des reptiles. Bijdragen tot de Dierkunde, 37:61–79.

———. 1976. Comparative histology of the endocrine glands, nasal cavities and digestive tract in anguimorph lizards. Pp. 205–278, *in* Morphology and Biology of Reptiles (A. Bellairs and C. Cox, eds.). Linnean Society Symposium Series 3.

Savage, J. M. 1963. Studies on the lizard family Xantusiidae. Los Angeles County Museum, Contributions in Science, 71: 1–38.

Schatzinger, R. 1975. Later Eocene (Uintan) lizards from the Greater San Diego area, California. Unpublished M.Sc. Thesis, San Diego State University, San Diego, California.

———. 1980. New species of *Palaeoxantusia* (Reptilia: Sauria) from the Uintan (Eocene) of San Diego County, California. Journal of Paleontology, 54:460–471.

Schmidt, K. P. 1919. Herpetology of the Belgian Congo. Bul-

letin of the American Museum of Natural History, 39:385–624.

SCHWENK, K. 1988. Comparative morphology of the lepidosaur tongue and its relevance to squamate phylogeny. Pp. 569–598, *in* Phylogenetic Relationships of the Lizard Families (R. Estes and G. Pregill, eds.). Stanford University Press, Stanford, California.

SEIFFERT, J. 1973. Upper Jurassic lizards from central Portugal. Servicos Geológicos de Portugal, Separata da Memória 22: 1–85.

SHEEHAN, P. M., AND D. E. FASTOVSKY. 1992. Major extinctions of land-dwelling vertebrates at the Cretaceous–Tertiary boundary, eastern Montana. Geology, 20:556–560.

SIMPSON, G. G. 1948. The beginning of the Age of Mammals in South America. Bulletin of the American Museum of Natural History, 91:1–232.

SLOAN, R. E. 1987. Paleocene and latest Cretaceous mammal ages, biozones, magnetozones, rates of sedimentation, and evolution. Pp. 165–200, *in* The Cretaceous/Tertiary Boundary in the San Juan and Raton Basins, New Mexico and Colorado (J. E. Fassett and J. K. Rigby, Jr., eds.). Geological Society of America, Special Paper 209, Boulder, Colorado.

SLOAN, R. E., AND L. VAN VALEN. 1965. Cretaceous mammals from Montana. Science, 148:220–227.

SMITH, H. M. 1946. Handbook of Lizards. Comstock Publication Co., Inc., New York, New York.

STANTON, T. W. 1910. Fox Hills sandstone and Lance Formation ("Ceratops beds") in South Dakota, North Dakota, and eastern Wyoming. American Journal of Science, Series 4, 30: 172–188.

STERNBERG, C. M. 1951. The lizard *Chamops* from the Wapiti Formation of northern Alberta; *Polyodontosaurus grandis* not a lizard. Bulletin of the National Museum of Canada, 123:256–258.

STORER, J. E. 1991. The mammals of the Gryde local fauna, Frenchman Formation (Maastrichtian: Lancian), Saskatchewan. Journal of Vertebrate Paleontology, 11:350–369.

STOTT, D. F. 1975. The Cretaceous System in northeastern British Columbia. Pp. 441–467, *in* The Cretaceous System in the Western Interior of North America (W. G. E. Caldwell, ed.). The Geological Association of Canada, Special Paper 13.

SULIMSKI, A. 1972. *Adamisaurus magnidentatus* n. gen., n. sp. (Sauria) from the Upper Cretaceous of Mongolia. Palaeontologia Polonica, 27:33–40.

———. 1975. Macrocephalosauridae and Polyglyphanodontidae (Sauria) from the Late Cretaceous of Mongolia. Palaeontologia Polonica, 33:25–102.

———. 1978. New data on the genus *Adamisaurus* Sulimski 1972 (Sauria) from the Upper Cretaceous of Mongolia. Palaeontologia Polonica, 38:43–56.

SULLIVAN, R. M. 1979. Revision of the Paleogene genus *Glyptosaurus* (Reptilia, Anguidae). Bulletin of the American Museum of Natural History, 163:1–72.

———. 1981. Fossil lizards from the San Juan Basin, New Mexico. Pp. 76–88, *in* Advances in San Juan Basin Paleontology (S. G. Lucas, J. K. Rigby, Jr., and B. Kues, eds.). University of New Mexico Press, Albuquerque, New Mexico.

———. 1982. Fossil lizards from Swain Quarry, "Fort Union Formation," middle Paleocene (Torrejonian), Carbon County, Wyoming. Journal of Paleontology, 56:996–1010.

———. 1986*a*. The skull of *Glyptosaurus sylvestris* Marsh, 1871 (Lacertilia: Anguidae). Journal of Vertebrate Paleontology, 6:28–37.

———. 1986*b*. A new fossil anguid lizard *Parodoxosaurus sanjuanensis,* new genus, new species from the middle Paleocene (Torrejonian) Nacimiento Formation, San Juan Basin, New Mexico. Journal of Herpetology, 20:109–111.

———. 1987. *Parophisaurus pawneensis* (Gilmore, 1928) new genus of anguid lizard from the middle Oligocene of North America. Journal of Herpetology, 21:115–133.

———. 1991. Paleocene Caudata and Squamata from Gidley and Silberling Quarries, Montana. Journal of Vertebrate Paleontology, 11:293–301.

TANKE, D. 1988. Ontogeny and dimorphism in *Pachyrhinosaurus* (Reptilia, Ceratopsidae), Pipestone Creek, N. W. Alberta, Canada. Journal of Vertebrate Paleontology, 8:27A, Supplement to No. 3: Abstracts of Papers, 48th Annual Meeting, Society of Vertebrate Paleontology, Tyrrell Museum of Palaeontology, Drumheller, Alberta, Canada.

THOMAS, R. G., D. A. EBERTH, A. L. DEINO, AND D. ROBINSON. 1990. Composition, radioisotopic ages, and potential significance of an altered volcanic ash (bentonite) from the Upper Cretaceous Judith River Formation, Dinosaur Provincial Park, southern Alberta, Canada. Cretaceous Research, 11: 125–162.

TOKARYK, T. T., AND P. C. JAMES. 1989. *Cimolopteryx* sp. (Aves, Charadriiformes) from the Frenchman Formation (Maastrichtian), Saskatchewan. Canadian Journal of Earth Sciences, 26:2729–2730.

TWENTE, J. W. 1952. Pliocene lizards from Kansas. Copeia, 1952:70–73.

VOROBYEVA, E. I., AND T. J. CHUGUNOVA. 1986. The dental system in lizards: An intergrated approach. Pp. 315–318, *in* Studies in Herpetology (Z. Roček, ed.). Prague, Czechoslovakia.

WALDMAN, M. 1970. A teiid lizard jaw from the Cretaceous of Alberta, Canada. Canadian Journal of Earth Sciences, 7: 542–547.

WALL, J. H. 1975. Diatoms and radiolarians from the Cretaceous System of Alberta—A preliminary report. Pp. 391–410, *in* The Cretaceous System in the Western Interior of North America (W. G. E. Caldwell, ed.). The Geological Association of Canada, Special Paper 13.

WILLIAMS, G. D., AND C. F. BURKE. 1964. Upper Cretaceous. Pp. 169–189, *in* Geological History of Western Canada (R. G. McCrossan and R. P. Glaister, eds.). Alberta Society of Petroleum Geology, Calgary, Alberta, Canada.

WILLIAMS, G. D., AND C. R. STELCK. 1975. Speculations on the Cretaceous palaeogeography of North America. Pp. 1–20, *in* The Cretaceous System in the Western Interior of North America (W. G. E. Caldwell, ed.). The Geological Association of Canada, Special Paper 13.

WILSON, M. V. H. 1988. Taphonomic process: Information loss and information gain. Geoscience Canada, 15:131–148.

WINKLER, D. A., P. A. MURRY, AND L. L. JACOBS. 1990. Early Cretaceous (Comanchean) vertebrates of central Texas. Journal of Vertebrate Paleontology, 10:95–116.

YATKOLA, D. A. 1976. Fossil *Heloderma* (Reptilia, Helodermatidae). The University of Kansas, Occasional Papers of the Museum of Natural History, 51:1–14.

ZANGERL, R. 1944. Contributions to the osteology of the skull of the Amphisbaenidae. American Midland Naturalist, 31: 417-454.